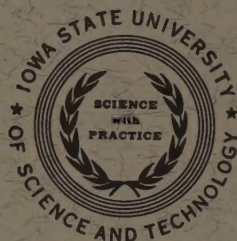


IOWA STATE JOURNAL OF SCIENCE

A Quarterly of Research

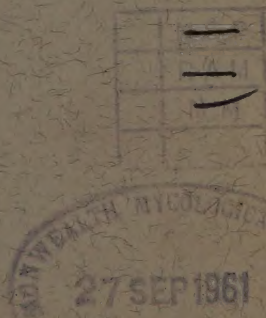


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TAXONOMY AND DISTRIBUTION OF THE GENUS *PHALARIS*^{1, 2}

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ABSTRACT. A cytotaxonomic study of the grass genus *Phalaris* including keys, synonymies, descriptions, illustrations and distributions of the fifteen species in the genus. A list of all previously reported chromosome numbers and new counts obtained by the author is included.

Four major evolutionary trends are recognized in the genus on the basis of morphological characters and cytological evidence.

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Over a century has passed since the last attempt to monograph the genus *Phalaris*. The treatments of the genus presented by earlier authors were not in agreement as to delimitation of taxa involved nor were their uses of taxonomic criteria uniform.

Members of this genus have been collected on every major land mass except Antarctica and Greenland. Likewise, the range of habitats is broad. Species of *Phalaris* are found at altitudes ranging from well below sea level to many thousands of feet above sea level. Some are dwellers of low, wet, marshy areas; others are found in areas that are dry throughout much of the year.

Certain species are dominant in the native vegetation of broad areas; others are ballast waifs and strays that have encircled the globe in their travels. At least three species have become weeds in waste-places in many parts of the world.

Some members of *Phalaris* have been widely used as forage grasses and as waterway control grasses. The seeds of one species are harvested commercially as a source of food for pet birds.

¹ Journal Paper No. J-4065 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1136. The facilities of the Iowa State University Herbarium, supported by the Industrial Science Research Institute, were used in the preparation of this paper.

² Based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Iowa State University, March, 1960.

³ During the terminal year of graduate study, the author was the recipient of a National Science Foundation Cooperative Fellowship. Many of the studies undertaken would not have been possible without its aid which is sincerely appreciated.

MATERIALS AND METHODS

Specimens were obtained from the institutional herbaria listed below as well as the author's collections. The key letters preceding each institution are the abbreviations given by Lanjou and Stafleu (1956). These abbreviations will be used hereafter whenever reference to a particular herbarium is necessary.

PH	Academy of Natural Sciences of Philadelphia
LE	Botanical Institute of the Academy of Sciences of the U.S.S.R.
MO	Missouri Botanical Garden
F	Chicago Natural History Museum
GH	Harvard University, Gray Herbarium
ISC	Iowa State University, Ames, Iowa
LINN	Linnean Society of London
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, France
PR	National Museum, Praha, Czechoslovakia
NY	New York Botanical Garden
NDA	North Dakota Agricultural College
L	Rijksherbarium, Leiden, Netherlands
SIGMA	Station Internationale de Géobotanique Méditerranéenne et Alpine, Montpellier, France
US	United States National Museum
NAP	Università di Napoli, Napoli, Italy
SDU	University of South Dakota

Field studies and collections of plants for herbarium specimens were made by the author in June and July, 1958, in Iowa, Minnesota, and Oklahoma. Further collections were made in Minnesota and Nebraska in June, 1959. Herbarium specimens were prepared from fresh material. Overnight drying of plants in presses placed on a portable electric dryer produced dry specimens suitable for storage.

The cooperation of the Regional Plant Introduction Station in Ames in providing seeds of many of the species of *Phalaris* greatly facilitated cytological and morphological studies in the genus. Dr. Beecher Crampton of the University of California, Davis, kindly furnished seeds of several species growing in California.

Collections of inflorescences for cytological studies commenced as soon as plants in the greenhouse began to bloom. As each inflorescence was removed and fixed, a coded tag was affixed to that particular culm. If cytological studies of florets of this inflorescence were successful, a voucher specimen of this tagged material was made. Any remaining material from the fixed inflorescence was dried and deposited with the voucher. Thus each voucher specimen consists of not only the plant from which an inflorescence was taken but also portions of the actual inflorescence used in cytological studies. A portion of the original seed sample from which any given specimen was grown was placed in an envelope and affixed to the voucher specimen. No chromosome numbers without confirming voucher specimens are presented in this paper. All voucher specimens are deposited in the herbarium of Iowa State University.

Complete synonymies are given for each species. Evidence for treatment of the names as synonyms is given by a brief statement. If no explanatory statement is given, then the description accompanying the original publication of the name was used as evidence. Excluded or unidentified names are presented in the Appendix of this paper.

A list of selected specimens examined is provided for each species. Specimens duplicated in several herbaria were used in this listing whenever possible.

THE GENUS PHALARIS

Taxonomic Considerations

Phalaris L. Sp. Pl. 54. (1753)

Typhoides Moench. Meth. Pl. 202. (1794)

Baldingera Gaertn., Mey., and Scherb. Fl. Wett. 1:96. (1799)

Digraphis Trin. Fund. Agrost. 127. (1820)

Phalaridantha Cariot. Et. Fleurs. 900. (1889)

Endallex Raf. ex Jacks. Ind. Kew. 1:839. (1893)

Description

Plants annual from fibrous underground roots or perennial from a dense crown or vigorous underground rhizomes; culms erect, terete; uppermost sheaths somewhat dilated distally; ligule up to 12 mm in height, membranous, truncate; blades linear, flat; panicle ovoid, sub-ovoid, or cylindrical, unbranched or with a few short, closely-appressed branches at base; spikelets 30 to several hundred, laterally compressed, 1-flowered, the single fertile floret subtended by 1 or 2 sterile florets; disarticulation above the glumes; glumes usually glabrous, rarely hirsute, equal or subequal, naviculate to acuminate, often keeled, the keel frequently broadened into a wing, wing margin entire, erose, or denticulate; sterile florets 1 or 2 or obsolete, subulate to somewhat swollen to chaffy, usually pubescent; fertile lemma coriaceous to indurate, glabrous or pubescent, often shiny; palea thin and delicate, obscurely 2-nerved, glabrous; stamens 3; stigmas 2, plumose; fruit somewhat flattened and elongated; basic chromosome number 6 or 7; diploids, tetraploids, pentaploids, hexaploids, and aneuploids.

Type of the genus: Phalaris arundinacea L. (Britton and Brown, 1913).

History of the genus

The earliest mention of Phalaris is possibly that of Dioscorides in the first century A.D. (see translation by Goodyer, transcribed by Gunther, 1954). Dioscorides refers to a plant with stalks that are knotty, reed-like and much like Zea in over-all appearance ("Zea," in Dioscorides' terminology, was Triticum, perhaps T. diococcum). On the basis of Dioscorides' description it does not seem possible to assign this plant positively to Phalaris. The drawing accompanying the description was made by a Byzantine artist circa 525 A.D. and provides no information as to the identity of Dioscorides' plant.

A description similar to that of Dioscorides by Matthioli (1554) likewise cannot be positively assigned to Phalaris.

Bauhin (1623) listed two phrase-names in Phalaris. Both of these phrase names were included by Linnaeus (1753) in synonymy under P. canariensis. One of Bauhin's names, Phalaris major semine nigro was described as "quo Canarios passeris praecipique nutriunt" and was reported as occurring in the "Canariis insulis."

Raius (Ray), in 1694, extended the range of the grasses mentioned by Bauhin to include Messina in Sicily, Baias and Neapolini (Naples) in Italy, and Monspelium in Gallia (France).

Linnaeus (1745) included two species of Phalaris in his treatment of the flora of Sweden. The first of these, identified by the phrase name Phalaris panicula oblonga, was treated as a synonym under Phalaris arundinacea in later works by the same author. The second species, Phalaris spica cylindrica, was later given as a synonym of Phalaris phleoides by Linnaeus.

In Linnaeus' Materia Medica (1749), a species with the name Phalaris panicula subovata spiciformi, glumis carinatis was listed as providing food (nutriens) for small birds (aviculis) and growing in "Canariae, Hetruria, Hispania." This name was given as a synonym of Phalaris canariensis by Linnaeus in 1753.

The first valid, legitimate publication of Phalaris using the binomial system was in the first edition of Linnaeus' Species Plantarum (1753). Five species and one variety were included: P. canariensis, P. arundinacea, P. arundinacea var. picta, P. erucaeformis, P. phleoides, and P. oryzoides. The last three of the above named, P. erucaeformis, P. phleoides, and P. oryzoides, were subsequently transferred by other authors to Beckmannia, Phleum, and Leersia, respectively. Phalaris was placed in Triandria, Dignyia in Linnaeus' sexual system of classification. Five new species, P. aquatica, P. bulbosa, P. utriculata, P. tuberosa, and P. paradoxa were described by Linnaeus in later editions of the Species Plantarum and in other works before his death in 1778.

Lamarck (1783, p.92) reviewed Phalaris and included twenty-one species. Lamarck's description of the genus is as follows:

Les fleurs sont glumacées, & ont leur bête extérieure uniflore, composée de deux valves égales, opposées, concaves, & tranchantes sur leur dos; leur bête interne, bivalve & plus petite que l'extérieure; trois étamines munies d'anthères oblonques; & un ovaire arrondi, chargé de deux styles capillaires, dont les stigmates sont velus.

Le fruit est une semence arrondie, un peu en pointe à ses deux bouts, lisse, & recouverte par la bête interne de la fleur que ne s'ouvre point.

Les Alpistes different des Fléoles, en ce qu'ils n'ont point leur bête extérieure tronquée à son sommet, & terminée par deux dents aiguës. On les distingue particulièrement par leur bête extérieure uniflore, souvent aplatie sur les côtés, & dont deux valves sont tranchantes sur leur dos.

No mention was made of the characteristic sterile florets found in the genus.

Using the above as a basis for delimiting Phalaris, it is not surprising that over one-half of the species included by Lamarck were in genera other than Phalaris, mostly Phleum but possibly also Agrostis, Leersia, Beckmannia, Pennisetum, Alopecurus, Koeleria, Polypogon, Heleocholea, and Panicum. The circumscription of Phalaris without using the sterile florets and coriaceous lemmas was not unique with Lamarck; no author previous to that time had even noted their occurrence.

Trinius (1828) included descriptions and illustrations of nine species in the genus. All of the species in Trinius' work were members of Phalaris as now delimited. This was the first taxonomic treatment of the genus to make use of the sterile florets as important generic characters.

Kunth (1833) included nineteen species in his synopsis of Phalaris. Of these species, ten were treated as "species genuinae," two were considered "species anomalaе," and seven listed in "species dubiaе." All of the members of the first two groups mentioned are species or varieties of Phalaris in its present sense while three of the last-mentioned group are in other genera.

The most extensive and critical review of the genus is that of Trinius (1840) in his monograph of the Phalarideae. Trinius treated fifteen species in this work, giving excellent descriptions for the most part, including a short key, and providing brief synonymies.

Steudel (1841) lists one hundred thirty-eight names that had been connected with Phalaris prior to that time. Most of the names were treated as synonyms; only twenty species were recognized. In a later work (1855) Steudel listed twenty-five species in the genus and included a short description of each.

Since 1855, no monographic study has been made of Phalaris on a world-wide basis. There have been, however, occasional treatments of certain groups of species such as Jansen and Wachter's treatment of Netherland's species (1916), Parodi's revision of Chilean species (1939), Ruiz' study on the species of Phalaris in Spain (1947), and Hitchcock's work on Phalaris in the United States (1950).

Paleobotany

Brues and Brues (1909, p.170) described the fossil species Melica primaeva based upon an impression collected by T.D.A. Cockerell in the Miocene shales at Florissant, Colorado. The illustration accompanying the description shows a series of bract-like structures clustered about a short axis. A portion of their original description is as follows:

The specimen shows a detached pair of second spikelets viewed from the inner, or side nearest the rachis. The spikelet which is best preserved is about 12 millimeters long and shows five glumes; the lower of these, presumably one of the empty glumes, is visible only at the base, its apical portion extending under the shale beneath the lowest flowering glume. The latter is not well preserved at the tip, but the second is visible for its entire length. It is 10 mm. long and about 2 mm. wide, broadly lanceolate in outline, with acutely pointed but unawned apex. Between the second and third flowering glumes can be seen the apex of the second empty glume. The spikelet thus appears to be three flowered, which also appears to be true of the second one . . .

This specimen was identified as a member of the genus Melica by Brues and Brues because of the "second insertion of the two spikelets as shown in the type, their large size and the form of the glumes, and the apparently very short joints of the rachilla."

MacGinitie (1953), in his review of the fossil plants of the Florissant beds, rejects Melica primaeva Brues and Brues saying that the specimen was too poor for identification.

Beetle (1958) transferred Melica primaeva to Phalaris as Phalaris primaeva (Brues and Brues) Beetle. Beetle lists the following features as a basis for putting this fossil in Phalaris: lack of awns, lack of prominent veins, comparatively wide glumes, lemmas, and paleas, comparative size of glume to lemma, comparative size of lemma to palea, and paired grouping of florets.

On the basis of the illustration accompanying Brues and Brues' description the present author can make no attempt at classifying the structure. Certainly two of the reasons that Beetle gave for placing this fossil in Phalaris, namely lack of prominent veins and paired grouping of florets, do not seem to be valid. Many species in Phalaris have rather prominent veins in the glumes. The paired grouping of florets is not a characteristic of Phalaris. One of the characters separating Phalaris from many other genera of grasses is that it has only one floret. It would seem that the taxonomic recognition of a fossil species on the basis of such meager evidence is unwarranted.

A second fossil from the Miocene shales of Florissant, Colorado was assigned to Phalaris by Cockerell (1913, p. 76). This species, named Phalaris (?) geometrorum by Cockerell, is based upon a single structure bearing a nebulous resemblance to a lemma.

MacGinitie (1953) transferred P. geometrorum to the gymnospermous genus Torreya, as T. geometrorum (Cockerell) MacGinitie. The photographs of the holotype and hypotype provided by MacGinitie leave no doubt that this fossil should not be classified as a member of Phalaris.

Cytology and cytogenetics

A summary of chromosome numbers reported for this genus by previous authors and those reported in this paper by the present author is presented in Table 1. The somatic number is given in all cases. It may either have been directly observed or calculated from observations of meiosis in pollen mother cells. With the exception of the author's counts, no verification of voucher specimens for other reported numbers has been made. No specific voucher specimen citations accompanied many of the chromosome counts reported by other authors. Pertinent data for the author's chromosome counts are presented under the corresponding species in the taxonomic treatment following.

Referring to Table 1, it will be seen that two basic chromosome numbers have been reported in this genus. One group, including P. angusta, P. arundinacea, P. californica, P. caroliniana, P. coerulescens, P. lemmonii, P. minor, P. paradoxa, P. platensis, and P. aquatica, has a basic number of $x=7$; the other group, including P. brachystachys, P. canariensis, and P. truncata, has a basic number of $x=6$.

Avdulov (1931) suggested that the $x=6$ number of P. canariensis resulted from the loss of a chromosome in an $x=7$ form. Darlington (1937)

Table 1. Summary of chromosome numbers reported in the genus Phalaris.

Species	2n	Reference
<u>P. angusta</u>	14	Saura (1943), Ambathsa (1956), present author
<u>P. arundinacea</u>	14	Church (1929)
	28	Avdulov (1931), Jenkin and Sethi (1932), Trumble (1935), Parthasarathy (1939), Hutton (1953), Tateoka (1954), Ambathsa (1956), Carnahan and Hill (1956), present author
	27-31, 35	Hanson and Hill (1953)
	29	Ambathsa (1956)
	42	Brock (unpublished, cited in Darlington and Wylie, 1955)
	56	Carnahan and Hill (1956) (experimentally produced polyploid)
<u>P. arundinacea</u> x		
<u>P. aquatica</u>	28	Jenkin and Sethi (1932), Ambathsa (1956)
	35, 42	Ambathsa (1956)
<u>P. brachystachys</u>	12	Miege (1939), Parthasarathy (1939), present author
<u>P. californica</u>	28	Stebbins and Love (1941), Ambathsa (1956)
<u>P. canariensis</u>	12	Church (1929), Avdulov (1931), Katterman (1931), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Ambathsa (1956), present author
<u>P. canariensis</u>	28	Nakajima (1933)
<u>P. caroliniana</u>	14	Brown (1950), Ambathsa (1956)
<u>P. coerulescens</u>	14	Trumble (1935), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Hutton (1953), Ambathsa (1956), present author
	28	Miege (1939)
<u>P. coerulescens</u> x		
<u>P. minor</u>	21	Hutton (1953) (F ₁ hybrid)
	42	Hutton (1953) (experimentally produced allopolyploid)
<u>P. lemmonii</u>	14	Parthasarathy (1939), present author
<u>P. minor</u>	28	Avdulov (1931), Trumble (1935), Miege (1939), Parthasarathy (1939), Hutton (1953), Ambathsa (1956)
	28, 29	Hanson and Hill (1953), present author
<u>P. minor</u> x		
<u>P. aquatica</u>	28	Hutton (1953) (F ₁ hybrid), Ambathsa (1956)
	56	Hutton (1953) (experimentally produced allopolyploid)
<u>P. paradoxa</u>	14	Avdulov (1931), Trumble (1935), Miege (1939), Parthasarathy (1939), Hanson and Hill (1953), Ambathsa (1956), present author
<u>P. platensis</u>	14	Ambathsa (1956)
<u>P. truncata</u>	12	Ambathsa (1956), present author
<u>P. aquatica</u>	28	Jenkin and Sethi (1932), Trumble (1935), Miege (1939), Parthasarathy (1939), Hanson and Hill (1953), Hutton (1953), Ambathsa (1956), present author

demonstrated that conditions favoring loss or gain of a chromosome can be produced by means of unequal translocations. In a study of the cytology of the Phalarideae, Parthasarathy (1939) reported that one pair of chromosomes in the 12-chromosome group is definitely longer than the other pairs. Parthasarathy suggests that the 12-chromosome types are derived from the 14-chromosome types by the fusion of two pairs of chromosomes with subterminal constrictions to give one pair with median constrictions. The chromosome complements of P. truncata, P. brachystachys, and P. canariensis ($2n=12$) in material studied by the author did not show much variation in the size of the chromosomes; all appeared to be about the same size. Ambathsa (1956), in an extensive treatment of the cytology of Phalaris, also suggests that the 12-chromosome types were derived from the 14-chromosome types by the fusion of two chromosomes, but proposes that one had a median centromere and the other had a terminal centromere. Ambathsa submits that the terminal centromere chromosome could fracture, lose its centromere and, subsequently, fuse with a median-centromere chromosome to produce a single chromosome with a submedian centromere. Stebbins (1950) states that it is impossible to change the basic number through simple transverse fragmentation and end-to-end fusion of single chromosomes. He further states that reduction of basic chromosome number must involve loss of a centromere plus at least a small amount of adjacent chromosomal material. Much evidence seems to indicate that a chromosome with two centromeres cannot function properly. Until experimental evidence can be introduced into the problem of chromosome number reduction in Phalaris, the author is unable to suggest which, if any, of the above suggested mechanisms have been in operation in this genus.

Ambathsa (1956) divided the $n=6$ chromosome group into two parts: (1) species with "I" shaped chromosomes, including P. brachystachys and P. canariensis and (2) species without "I" shaped chromosomes, including P. truncata. These groupings do not reflect the morphological relationships between the species involved. P. brachystachys and P. truncata are very similar (see Plate 6 and Table 10), the most obvious difference being that the former is an annual and the latter a perennial. P. canariensis possesses features not found in either of the other two, the most prominent being the chaffy sterile florets (Plate 6, c).

Ambathsa proposed two major subdivisions in the $x=7$ group. One subdivision, including P. angusta, P. californica, P. caroliniana, P. lemmonii, P. paradoxa, and P. platensis, has a haploid chromosome number of $n=7$; the other subdivision, including P. minor and P. tuberosa has a haploid number of $n=14$. P. arundinacea and P. coerulescens have both $n=7$ and $n=14$ as haploid numbers within the population.

Ambathsa further divides the $n=7$ group into two categories: (1) those species with no "J" or "I" shaped chromosomes (P. coerulescens) and (2) those species with "J" or "I" shaped chromosomes (P. paradoxa, P. caroliniana, P. angusta, and P. platensis). These groupings appear to agree only partially with the morphological evidence as to relationships. P. paradoxa and P. coerulescens, separated on the basis of chromosome shapes, are very similar morphologically. The main difference between these two is that the former is an annual, the latter a perennial. P. caroliniana, P. angusta, and P. platensis are somewhat

similar to one another but do not seem to be closely related with respect to spikelet morphology and geographic distribution.

Ambathsa proposed that the $n=7$ group is the basic stock from which other species in Phalaris have been derived. He further suggests three major developmental trends from this stock: (1) a decrease in chromosome number to $n=6$, resulting in such species as P. brachystachys, P. canariensis, and P. truncata, (2) doubling of chromosome number by autotetraploidy, as in P. minor, and (3) doubling of chromosome number by allotetraploidy, as in P. arundinacea. Five species, P. coerulescens, P. paradoxa, P. caroliniana, P. angusta, and P. platensis, have retained the $n=7$ number and have undergone specialization at this level.

Stebbins (1950) has suggested that autopolyploidy is not commonly found in nature and states that many of the supposed autopolyploids are actually of hybrid origin. Further work is needed in the polyploid species of Phalaris to determine the nature of ploidy in this genus.

The names of P. nodosa, P. tuberosa, and P. aquatica, as used by Ambathsa, cannot be identified. Ambathsa did not make any voucher specimens for his chromosome counts and did not cite any references used for the identification of the species studied. Apparently Ambathsa used the names on the seed packets he received from Australian plant introduction services.

Seven of the thirteen species that have been studied cytologically are diploid annuals (P. angusta, P. brachystachys, P. canariensis, P. caroliniana, P. lemmonii, P. paradoxa, and P. platensis); one is a diploid perennial (P. truncata); two were tetraploid perennials (P. californica and P. aquatica). Two of the perennials, P. arundinacea and P. coerulescens, are represented by both diploids and polyploids.

Stebbins (1950, p. 468) states that the annual, specialized species of Phalaris (Stebbins gave P. canariensis and P. paradoxa as examples) have smaller chromosomes than the perennial, generalized species (Stebbins gave no examples). The present author is unable to corroborate this statement. Material of P. canariensis available for study had some of the largest chromosomes of any of the species examined. The chromosomes of P. paradoxa, an annual, were relatively small, but barely smaller than those of P. arundinacea and P. truncata both of which are perennials. P. paradoxa chromosomes were actually larger than the chromosomes of P. aquatica and P. coerulescens which are also perennials. Ambathsa (1956) likewise found many annual species of Phalaris whose mean chromosome size exceeded that of the perennials.

There have been several successful attempts at producing interspecific hybrids in Phalaris. Of these hybrids, only two have been examined cytologically. These are: P. aquatica x P. arundinacea and P. aquatica x P. minor. The results of these studies are presented in the taxonomic treatment of these species.

Drawings of meiotic figures in species studied by the author are presented in Plate 1.

Phylogenetic considerations: generic level

The reduction patterns displayed in the spikelets and inflorescences of Phalaris have perplexed grass phylogenists for years but have stimulated investigation of the floral anatomy and development in only one

Plate 1. Meiotic figures in Phalaris

- a. P. paradoxa, $2n=14$
- b. P. coerulescens, $2n=14$
- c. P. minor, $2n=28$
- d. P. arundinacea, $2n=28$
- e. P. aquatica, $2n=28$
- f. P. truncata, $2n=12$
- g. P. brachystachys, $2n=12$
- h. P. canariensis, $2n=12$
- i. P. angusta, $2n=14$
- j. P. lemmonii, $2n=14$



species. Holt (1954) made a detailed study of the initiation and development of the inflorescence of *P. arundinacea*. He demonstrated that the fertile floret is ontogenetically lateral and not terminal as commonly interpreted. The two lowermost florets are much reduced; the third floret is fertile and develops normally; the uppermost floret never develops. Its apical meristem becomes highly vacuolated and soon becomes a mass of lignified tissue compressed between the palea and the subtending sterile floret. Thus it can be seen that the spikelet in *Phalaris* is indeterminate rather than determinate in development. Unfortunately the dearth of detailed ontogenetic studies in many genera of grasses, especially those with apparently determinate spikelets, prevents the broad use of anatomical development patterns in establishing intergeneric relationships.

Prat (1932, 1936), in a radical departure from the traditional system of classification based primarily upon inflorescence type and spikelet structure, emphasized various anatomical features in the formation of a classification of the grass family. Three subfamilies were recognized: Bambusoideae, Panicoideae, and Festucoideae. The Bambusoideae were characterized as having a complex leaf epidermis with papillae, warts and bicellular hairs. Members of the subfamily Panicoideae were reported to possess a complex leaf epidermis with bicellular or cushion-based hairs, silicified cells of complicated forms (hourglass or dumbbell shaped), rhomboid stomata, and basic chromosome numbers of 5, 6, or 9. The Festucoideae have a simple epidermis with silicified cells of a rounded or square shape, unicellular hairs, ovoid stomata, and a basic chromosome number of 7. On the basis of these characters, *Phalaris* is definitely a member of the Festucoideae in having all of the characters attributed to this subfamily. Some of the species of *Phalaris* have a basic chromosome number of 6, but it is probable that this is derived from an $x=7$ ancestor. Plate 2 shows the leaf epidermis of three species of *Phalaris*.

Reeder (1957) studied four embryo characters that seem to possess phylogenetic significance in the grass family. These characters and the corresponding observations made upon *Phalaris* by Reeder are presented in Table 2.

Stebbins (1956), in a review of previous work on grass phylogeny by various authors, suggests other criteria for estimating phyletic relationships in the Gramineae. Included in these are: relative size of embryo, nature of starch grains (simple or compound), chromosome size, and number and type of lodicules. *Phalaris* has relatively small embryos (for example, see Plate 6, d, *P. canariensis*), compound starch grains (Plate 2, e), relatively large chromosomes (Plate 1), and two, pointed lodicules (Plate 2, d). All of these are festucoid features.

For many years the tribe Phalarideae has been a repository for grass genera whose main distinguishing feature is the possession of one or more sterile or staminate florets subtending a single fertile floret. Hackel (1890), Bews (1929) and Hubbard (1944) included six genera in the Phalarideae: *Ehrharta*, *Microlaena*, *Tetrarrhena*, *Anthoxanthum*, *Heirochloë*, and *Phalaris*. Reeder (1957) reported that *Ehrharta* was panicoid with respect to three of the four embryo features studied. Tateoka (1957) placed *Ehrharta*, *Microlaena*, and *Tetrarrhena* in a new tribe, the

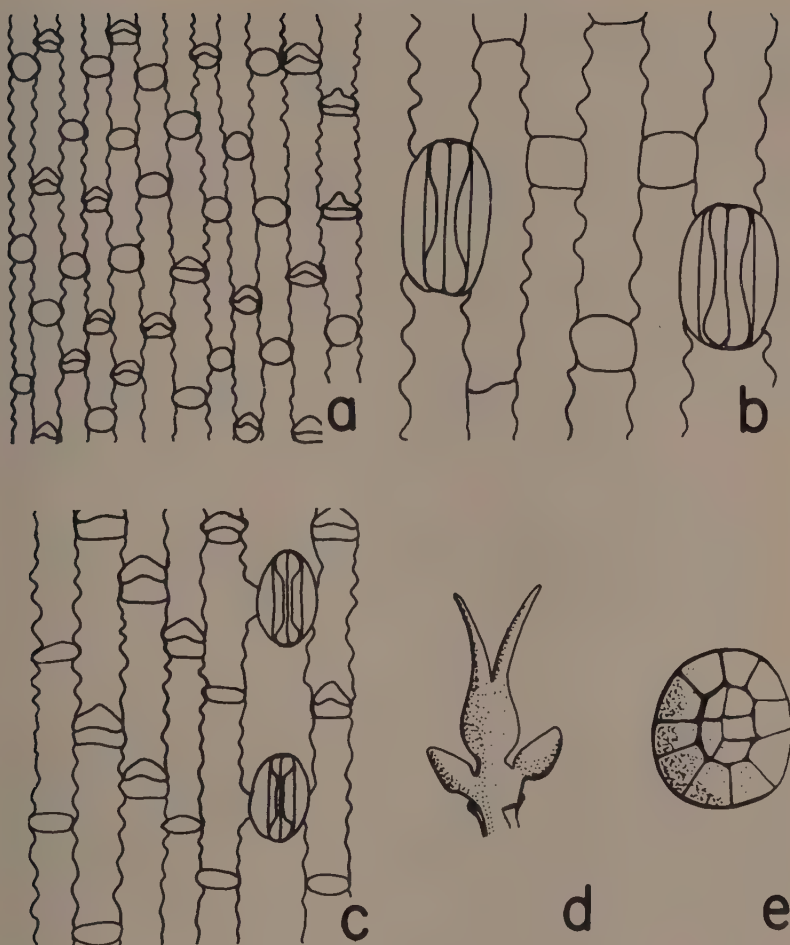


Plate 2. Glume epidermis, leaf epidermis, lodicules, and starch grains of Phalaris.

- a. Glume epidermis of P. canariensis
- b. Abaxial leaf surface of P. arundinacea
- c. Abaxial leaf surface of P. paradoxa
- d. Flower showing lodicules, P. arundinacea
- e. Starch grain, P. canariensis

Table 2. Synopsis of Reeder's observations on grass embryos.

Character	Festucoid	Panicoid	<u>Phalaris</u>
course of vascular system	coleoptile inserted at about the point where scutellum bundle diverges	coptile inserted some distance above the point of divergence of scutellum bundle	festucoid
epiblast (present or absent)	usually present in the Festucoideae	always absent in the Panicoideae	present
embryonic leaf	first embryonic leaf with few vascular bundles and margins which meet but do not overlap	first embryonic leaf with many vascular bundles and overlapping margins	festucoid
lower portion of scutellum	lower portion of scutellum absent or fused with the coleorhiza	distinct cleft between coleorhiza and lower portion of scutellum	festucoid

Ehrharteae and included it in the subfamily Arundoideae near the tribes Meliceae, Glycerieae, Stipeae, and Aristideae. Darlington and Wylie (1955) give the basic chromosome number of Ehrharta and Microlaena as $x=12$. On the basis of floral morphology, embryo structure, and chromosome number it seems probable that Ehrharta, Microlaena, and Tetrarrhena are not closely related to Phalaris, Hierochloë, and Anthoxanthum and should be segregated from them. Riecken (1929) studied spikelet morphology of selected species in Anthoxanthum, Hierochloë (referred to Torresia by Riecken), and Phalaris. Riecken reported that Anthoxanthum differs from the other two genera in having two stamens and no lodicules; Phalaris and Hierochloë both have three stamens and two lodicules. In addition Anthoxanthum has a basic chromosome number of $x=5$, while Hierochloë has $x=7$ and Phalaris has $x=6$ to 7. On the basis of this information, it seems that Anthoxanthum has its affinities elsewhere than with Phalaris and Hierochloë.

Phalaris and Hierochloë possibly represent steps in a reduction series with Hierochloë having staminate rudimentary florets and Phalaris having much reduced, sterile rudimentary florets.

In summary, it is evident that Phalaris has its strongest evolutionary ties with the festucoid trend of specialization within the Gramineae. The highly modified spikelet structure of Phalaris permits no more than speculation as to its relationship with other genera. It would seem probable that the hypothetical "pro-Phalaris" was a festucoid grass with rather large, wingless, or very narrowly winged, subequal glumes, four

florets, the upper floret being somewhat reduced, and a fairly dense, lobed panicle. These characters are all represented in other festucoid genera. Characters common to many festucoid genera are presumed to be primitive with respect to Phalaris. Those characters that are highly modified and restricted to Phalaris are presumed to be advanced. Reduction and specialization of several of these features has resulted in species with broadly winged glumes, highly reduced sterile florets, and ovoid or cylindrical inflorescences. A given species of Phalaris may possess some advanced features and, at the same time, retain some relatively primitive characters, e.g. Phalaris arundinacea has primitive features such as wingless glumes and a lobed inflorescence; advanced features include several levels of polyploidy and reduced, subulate, sterile florets.

Phylogenetic considerations: Infrageneric level

Since the hypothetical primitive Phalaris does not exist today, we can only speculate as to the relationships between the present-day species. A phylogenetic chart (Fig. 1) is provided as the basis of the following discussion.

The center of diversity of Phalaris is in the Mediterranean region. Seven of the fifteen species in the genus, including P. brachystachys, P. truncata, P. canariensis, P. coerulescens, P. paradoxa, P. minor, and P. aquatica, were probably restricted to this area prior to being distributed to other parts of the world by man (Fig. 2). P. minor has extended its range somewhat eastward from the Mediterranean, apparently along some of the old caravan routes.

The following four variations in the structure of the sterile florets have taken place in the Mediterranean species:

1. Reduced, swollen, sterile florets. Two species, P. brachystachys and P. truncata have sterile florets that are reduced to this form. The former is an annual, the latter a perennial. Thellung (1915) states that P. brachystachys is a weed that has evolved the annual habit in response to annual tilling of the soil. Thellung's explanation of the annual habit in this, as well as in other groups, may have some merit but it would seem necessary to obtain more precise data concerned with selective values and evolutionary rates before positive statements can be made with respect to this idea.

2. Bract-like, chaffy, sterile florets. The only species in this category is P. canariensis. This species approaches the presumed primitive form most closely in its sterile floret type (Plate 6, d). It must be pointed out that, while P. canariensis is perhaps primitive with respect to sterile florets, it is advanced as far as glume-wing development and reduced chromosome number are concerned.

3. Obsolete sterile florets. P. coerulescens, a perennial, and P. paradoxa, an annual, are the only two species represented in this trend. In these two species, the sterile florets are very reduced and consist of only a small amount of tissue at the base of the fertile floret. In addition to the extreme modification of the sterile florets, the spikelets tend to fall in groups, with one fertile spikelet surrounded by several staminate or sterile spikelets. P. paradoxa is highly variable in this respect and shows a number of subspecific groups.

4. Subulate sterile florets. On the basis of geographic distribution, this complex can be further divided into the following three lines of development: (1) Old World species, (2) circumboreal species, and (3) New World species.

Three Old World species, P. minor, P. aquatica, and P. maderensis, are included in the first line of development. All of these species have only one well-developed sterile floret. P. minor and P. aquatica are native to the Mediterranean region while P. maderensis is apparently restricted to the Madeira Islands, 450 miles northwest of Morocco. A possible explanation for this disjunct distribution is offered by Ridley (1930). Ridley suggests that the flora of the Canary, Cape Verde, and Madeira Islands is derived from the west coast of Africa by an ancient land connection. Another possible explanation for the distribution of P. maderensis is that the ancestral disseminules may have been carried over the oceanic gap by birds. Speciation in response to this new environment may subsequently have taken place.

The second line of development includes a single circumboreal species, P. arundinacea. This is the only species of Phalaris that has a natural range including both the Old and New Worlds. It seems possible that some taxon at least very similar to P. arundinacea may have given rise to the next developmental line treated, the New World species.

The New World species include P. californica, P. caroliniana, P. amethystina, P. lemmonii, P. platensis, and P. angusta. These six species appear to have evolved along four evolutionary trends as based upon their cytology and inflorescence and spikelet morphology.

The first of these trends includes only P. californica, a tetraploid perennial restricted to California and southern Oregon. Morphologically this species remained relatively unspecialized in retaining wingless glumes and the perennial habit.

The second evolutionary trend includes P. caroliniana and P. amethystina. These species are diploid annuals that have winged glumes, somewhat flattened fertile florets, and compact, ovoid inflorescences. P. caroliniana has a broad range that includes southern United States and northern Mexico. P. amethystina is restricted to central Chile, almost 4000 miles from the nearest station of P. caroliniana.

A third evolutionary trend contains two diploid annuals, P. lemmonii and P. platensis. These taxa have wingless glumes, inflated fertile florets, and somewhat cylindrical inflorescences. P. lemmonii is restricted to coastal valleys in California; P. platensis is found in northern Argentina and Uruguay.

The fourth trend includes the diploid annual species, P. angusta. This species has winged glumes, somewhat flattened fertile florets, and a very compact, cylindrical inflorescence. P. angusta is found in southern and western United States and in central South America.

Three of the four evolutionary trends discussed above contain taxa with disjunct distributions including North and South America. Stebbins (1950, p.544) suggests five ways in which a disjunct distribution can arise: (1) direct dispersal over a long distance (the so-called "sweepstakes dispersal" of Simpson), (2) dispersal over a shorter distance through wider distribution and greater proximity of the two areas in the

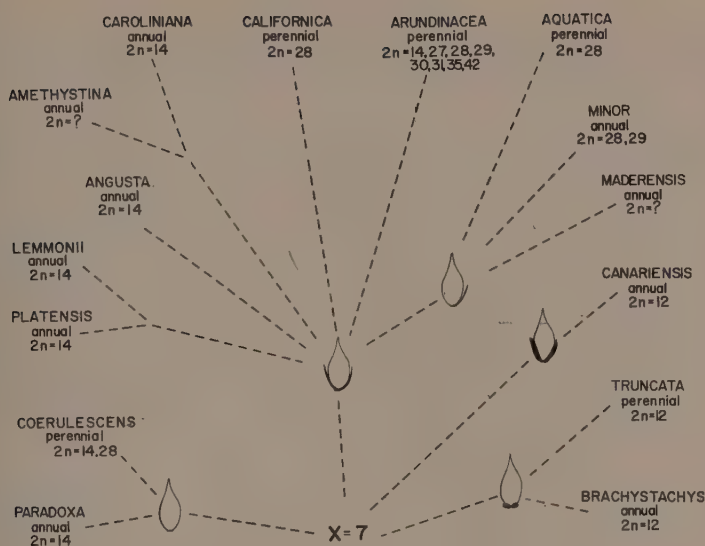


Figure 1. Possible phyletic relationships within the genus *Phalaris*.

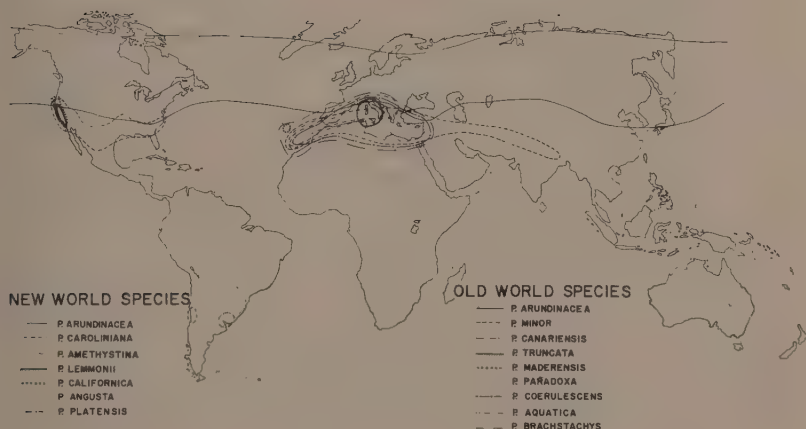


Figure 2. Geographic distribution of the genus *Phalaris*.

past, (3) wider distribution with complete continuity between the two areas in the past, (4) dispersal over a series of short distances by means of "stepping-stones," and (5) migration from a former area outside of the two present areas.

The first proposal, that of sweepstakes dispersal, seems quite possible. Grant (1959) suggests this as a solution to parallel distribution problems in certain taxa of the Polemoniaceae. In this group, as well as in *Phalaris*, a number of bird migratory routes coincide fairly well with the distributional patterns. Shore birds such as the Wilson phalarope, spotted sandpiper, killdeer, and snowy plover pass from western North America to coastal Peru, Chile, and Patagonia (Grant, 1959). In the Polemoniaceae the distribution of seeds is facilitated by a mucilaginous outer layer which may cause them to stick to the feathers of birds. The mode of dispersal in *Phalaris* would be quite different but fundamentally of the same level of importance. The species involved are commonly found in wet areas of grasslands, near pools, etc. These are the very same areas visited by shore birds in their migratory activities. It is entirely conceivable that *Phalaris* florets have been transported in the digestive tracts of shore birds from North America, particularly California, to South America. A relative of these species, *P. canariensis*, has been used in commercial birdseed preparations for many years so there is little reason to doubt the value of these seeds in bird feeding activities. The indurate lemma, which almost completely encloses the caryopsis and palea, could perhaps protect the fruit from digestive breakdown within the bird's system.

The second proposal of Stebbins, that of dispersal over a shorter distance through wider distribution and greater proximity to the two areas in the past, is certainly not without merit. This suggestion would seem to involve either a migration of similar nature to sweepstakes dispersal or a transtropical land migration. The latter alternative does not seem acceptable. If we assume that the tropics themselves, regardless of their size or latitudinal position in the past, were of substantially the same climatic character, then a taxon migrating from North to South America must adapt to gradually warmer and more humid climates on the way southward, finally reaching tropical conditions, then gradually reverse this adaptive trend as it emerges on the southern edge of the tropics and moves out onto the coastal areas and pampas. The ranges of the species involved are separated by at least 3000 miles at the present. However, geologic and climatic changes may well have destroyed the closer proximity possessed by the taxa in the past.

Stebbins' third proposal, a wider distribution with complete continuity between the two areas in the past, seems unlikely as an explanation of the disjunct distributions of species complexes in *Phalaris*. Grant (1959) rejected this suggestion for vicarious taxa in the Polemoniaceae. He asserts that, if temperate groups on opposite sides of the tropics diverged independently from a tropical ancestor, their systematic relationships with one another will not be particularly close since the evolutionary changes in passing from the ancestral group to either modern group would probably not progress in the same direction at the same speed. The present author is inclined to agree. Certainly it is difficult to conceive that a common ancestor could give rise to two separate complexes,

one in each hemisphere, each of which has its component species more closely related to species in the other hemisphere than to the other members of its complex.

The fourth alternative of Stebbins, that of dispersal over a series of short distances by means of "stepping-stones," cannot be summarily dismissed. In the geologic past the broadening areas of cool climates may have reduced the latitude of the tropics considerably. This could also mean that the higher elevations in the tropics may have been much more temperate in climatic character than at the present time. These temperate "stepping-stones" may have provided a means of migration allowing North American taxa to expand their ranges southward to similar environments. Present-day distributions in Phalaris provide little evidence for or against this proposal. Occasional collections of P. angusta have been made in the Colombian highlands but there is no assurance that these are relict rather than introduced populations.

The last-mentioned proposal of Stebbins, migration from a former area outside of the two present areas, seems quite improbable. If the so-called "former area" were temperate in climate, the migration pattern would involve movement through subtropics to tropics, thence, reversing the climatic change, back through subtropics to temperate regions. That a single taxon could be subjected to so many environmental and competitive changes and yet remain relatively unchanged seems rather remote. If the "former area" were tropic in nature, the migration pattern would be simpler, but, once again, it seems improbable that a taxon would evolve in the same direction and at roughly the same speed in two separate hemispheres.

A possibility that cannot be overlooked in explaining the vicarious species in Phalaris existing in North and South America is that they were derived from P. angusta or basic stock similar to it. P. angusta has a disjunct distribution embracing sections of both of these continents. The best argument against this proposal is that P. angusta itself seems to be a relatively advanced species whose morphologic specializations have taken a different evolutionary direction than either of the other species complexes. It appears quite possible that P. angusta has also been distributed from North to South America by migratory birds, but has not undergone morphologic speciation.

In summary, Phalaris has its center of diversity in the Mediterranean region. Initial evolution may have produced a series of complexes that were specialized not only in the unique characters of their sterile florets but also, in some instances, reduced chromosome numbers. Along with this initial specialization, a type arose which carried the generic characters almost entirely around the world in the northern hemisphere. This prototype, in its southward migration in the Americas, became specialized in a number of respects such as the development of winged glumes, ovoid or cylindrical inflorescences, and annual habit. Subsequent long distance dispersal may have carried the genus into South America where further speciation occurred.

Key to the Species of the Genus Phalaris

1. Fertile floret glabrous or with only a few hairs at the base of the sterile florets; sterile florets obsolete (0.1-0.2 mm long). 2
 2. Spikelets falling in groups of seven, one fertile spikelet surrounded by six sterile spikelets, the group falling as a unit; some sterile spikelets deformed and clavate; fertile lemma 2.7-3.3 mm long; caryopsis 2.2-2.8 mm long; annual plants with fibrous roots; culms not bulbous at base. 1. P. paradoxa
 2. Spikelets falling singly, not in groups of seven, or, if occasionally falling in groups, these not uniformly consisting of seven spikelets with more than 1 fertile spikelet per group; sterile spikelets not deformed or clavate; fertile lemma 2.9-4.2 mm long; caryopsis 2.4-3.5 mm long. perennial plants arising from a dense crown; culms blubous at base. 2. P. coerulescens
1. Fertile floret densely or sparsely pubescent; sterile florets usually at least one-third as long as fertile florets, if shorter, then more or less swollen and fleshy (see illustrations of P. truncata and P. brachystachys, Plate 6). 3
 3. Sterile floret one, well developed or obsolete. 4
 4. Sterile floret obsolete, less than 0.3 mm long. 3. P. minor
 4. Sterile florets well developed, more than 0.5 mm long. 5
 5. Glumes truncate; inflorescence narrowly cylindrical; caryopsis 1.6-1.8 mm long; known only from Madeira Islands (see illustrations, Plate 7, i-k). 11. P. maderensis
 5. Glumes acute to acuminate; inflorescence ovate-oblong to broadly cylindrical; caryopsis more than 2.2 mm long. 6
 6. Glume wings usually toothed or erose; annual plants with nonbulbous culm bases. 3. P. minor
 6. Glume wings usually entire; perennial plants from a dense crown; culm bases sometimes bulbous. 5. P. aquatica
 3. Sterile florets two. 7
 7. Sterile florets unequal, the longer 1.0-2.2 mm long, the shorter less than 0.5 mm long. 5. P. aquatica
 7. Sterile florets equal or nearly so. 8
 8. Sterile florets swollen and somewhat fleshy, less than 1 mm long (see illustrations of P. brachystachys and P. truncata, Plate 6). 9

9. Glumes 5.5-6.2 mm long, truncate; caryopsis 2.8-3.0 mm long, 1.2-1.3 mm wide; perennial plants arising from a dense crown. 6. P. truncata
9. Glumes 6.3-8.5 mm long, rather abruptly pointed and acute; caryopsis 3.5-3.9 mm long, 1.5-1.7 mm wide, annuals. 7. P. brachystachys
8. Sterile florets subulate or chaffy, usually more than 1 mm long. 10
10. Sterile florets broad and chaffy, not subulate; more than half as long as fertile lemma. 8. P. canariensis
10. Sterile florets subulate, usually less than one-half as long as fertile lemma. 11
11. Glumes not winged (very narrowly winged in P. californica). 12
12. Fertile floret turgid, nearly round in cross section, pubescence spreading; annuals; plants of California (adventive, Australia). 14. P. lemmonii
12. Fertile floret not turgid, usually elliptic in cross section, pubescence appressed; perennials with spreading, scaly rhizomes or arising from a dense tussock or annuals. 13
13. Inflorescence cylindrical, without truncate base, more than 2 times as long as broad; perennials from scaly rhizomes or annuals. 14
13. Inflorescence broadly ovate with truncate base, usually not more than two times as long as broad; perennial plant without rhizomes, arising from a dense crown; California or Oregon. 10. P. californica
14. Plants perennial from scaly rhizomes; inflorescence usually more than 5 cm long, lobed or branched at the base; caryopsis 2.0 mm long or less, mostly northern hemisphere. 15
15. Leaves longitudinally striped with white. 4a. P. arundinacea f. picta
15. Leaves uniformly green. 4b. P. arundinacea f. arundinacea
14. Plants annual from fibrous root system; inflorescence less than 4.5 cm long, not lobed or branched at the base; caryopsis 2.0 mm long or more; west coast of Chile. 12. P. amethystina
11. Glumes winged (very narrowly in P. californica). 16

16. Midnerve and lateral nerves of glumes sharply scabrous with many (9 or more) short stout hairs. 17
17. Fertile lemma turgid, the tip acuminate and glabrous. 18
18. Glumes 4.9-6.7 mm long; California. 14. P. lemmonii
18. Glumes 3.9-4.3 mm long; southern South America (adventive, Netherlands). 13. P. platensis
17. Fertile lemma more or less flattened; the tip acute and pubescent. 19
19. Inflorescence broadly ovate, usually not more than two times as long as broad; glume wing very narrow and inconspicuous; perennial plants arising from tussocks; caryopsis more than 2.4 mm long; California. 10. P. californica
19. Inflorescence cylindrical, usually three or more times as long as broad; glume wing broad and well developed; annual plant with fibrous roots; caryopsis less than 2.2 mm long. 20
20. Glumes acute to acuminate; caryopsis 2.1-2.2 mm long; southern South America. 12. P. amethystina
20. Glumes naviculate or truncate; caryopsis less than 1.8 mm long. 9. P. angusta
16. Midnerve of glumes scabrous with short, delicate barbs; lateral nerves glabrous or with only a few (less than 5) barbs. 21
21. Fertile lemma turgid, the tip acuminate and glabrous, pubescence spreading; caryopsis 2.1-2.3 mm long; California (adventive, Australia). 14. P. lemmonii
21. Fertile lemma more or less flattened, the tip acute, somewhat pubescent, pubescence of lower areas of lemmas appressed; caryopsis 1.4-1.6 mm long; southern United States west to California. 15. P. caroliniana
1. Phalaris paradoxa
Phalaris paradoxa L. Sp. Pl. ed.2. 2:1665. (1763) (Holotype in LINN; photograph of holotype in GH)
Phalaris praemorsa Lam. Fl. Franc. 3:566. (1778)
Phalaris pruinosa Lam. ex Beauv. Agröst. (1812) (Name given in index as synonym of P. paradoxa L.)
Phalaris appendiculata Roem. and Schult. Mant. 2:216. (1824)
Phalaris dentata Sieb. ex Roem. and Schult. Mant. 2:216. (1824)
(Name given as synonym of P. appendiculata Roem. and Schult.)

- Phalaris obvallata Trin. Mem. Acad. St.-Petersb. Ser. 6. 5:51. (1840) (Holotype in LE)
- Phalaris rubens Ehrenb. ex Trin. Mem. Acad. St.-Petersb. Ser. 6. 5:51. (1840) (Holotype in LE)
- Phalaris subthorpii Griseb. Spicil. Fl. Rumel. 2:468. 1843)
- Phalaris pseudo-paradoxa Fig. and De Not. Mem. Acc. Torin. Ser. 2. 14:11. (1853)
- Phalaris paradoxa var. intacta Coss. and Dur. Expl. Sci. Alger. 2:24. (1854)
- Phalaris paradoxa var. intermedia Coss. and Dur. Expl. Sci. Alger. 2:24. (1854)
- Phalaris paradoxa var. praemorsa (Lam.) Coss. and Dur. Expl. Sci. Alger. 2:25. (1854) (Based on P. praemorsa Lam.)
- Phalaris utriculosa L. ex Munro. Jour. Linn. Soc. 6:36. (1862) (Munro cites this name which is from Linnaeus' manuscript notes of Sp. Pl. ed. 1. A marginal note in the manuscript by Linnaeus equates this name to P. paradoxa.)
- Phalaris paradoxa var. appendiculata (Roem. and Schult.) Pirotta. Ann. Del R. Ist. Bot. Roma. 8:328. (1908) (Based on P. appendiculata Roem. and Schult.) (Duplicates of syntype in MO, US)
- Phalaris paradoxa f. nana Pirotta. Ann. del R. Ist. Bot. Roma. 8:328. (1908)
- Phalaris paradoxa var. megastachys Goiran. Nuov. Giorn. Bot. Ital. Nuova ser. Mem. Soc. Bot. Ital. 17:53. (1910)
- Phalaris paradoxa var. microstachys Goiran. Nuov. Giorn. Bot. Ital. Nuova ser. Mem. Soc. Bot. Ital. 17:53. (1910).
- Phalaris paradoxa var. typica Ruiz. Anal. Jard. Bot. Madrid. 8:486. (1947) (Based on Phalaris paradoxa L.)
- Phalaris paradoxa var. typica Ruiz f. praemorsa (Lam.) Ruiz. Anal. Jard. Bot. Madrid. 8:486. (1947)

Description

Annual, tufted, culms 20-100 cm tall; panicle up to 9 cm long and 2 cm wide, dense, oblong, tapering to narrow base; spikelets falling from the inflorescence in groups of 6 or 7, slender pedicelled, with 5 or 6 sterile spikelets clustered about a single fertile spikelet; sterile spikelets gradating from those with well-developed, narrowly-winged glumes up to 9 mm long to those in which all spikelet parts are reduced to clavate knobs of tissue terminating the pedicel; glumes of fertile spikelet 5.5-8.2 mm long, about 1 mm wide, acuminate to subulate, the nerves conspicuous, upper portion winged, the wing with a tooth-like projection near the middle; fertile florets of fertile spikelets 2.5-3.5 mm long, 0.8-1.5 mm wide, indurate, light-colored, shining, glabrous or with a few short hairs near the apex; sterile florets of fertile spikelets obsolete, represented only by knob-like projections at the base of the fertile floret; grain 2.3-2.6 mm long, 0.9-1.1 mm wide, subovoid to ellipsoid; somatic chromosomes $2n=14$, the chromosome ca. 3-5 μ long at diakinesis.

Observations

Members of this species are interesting in a number of respects. Some spikelets of the inflorescence are reduced and sterile. Usually the spikelets fall in groups of seven (occasionally six), with six (or five) sterile spikelets and one fertile spikelet.

There are three general types of sterile spikelets. For convenience the author has given these the identifying names clavate, reduced, and normal. The characters of these three kinds of sterile spikelets are presented below:

1. Clavate-sterile spikelets. Sterile spikelets of this group are very much reduced, the entire spikelet represented by a small club-shaped mass of tissue terminating the pedicel. These spikelets are always found at the base of the inflorescence (Plate 3, e).

2. Reduced-sterile spikelets. Spikelets of this group have glumes that are shorter than those of fertile spikelets in the same inflorescence. The glume tips are truncate in over-all outline and are erose (Plate 3, e).

3. Normal sterile spikelets. Sterile spikelets of this class are very similar to the fertile spikelets. The main difference between the two is that the fertile spikelets are quite swollen by the developing floret while the sterile spikelets are flattened and contain aborted florets (Plate 3, b, d).

Preliminary investigations within this species revealed a number of correlations between various features. In order that a more precise concept of this variation pattern might be obtained, the author measured and examined several characters on a total of seventy-one specimens from the same number of collection stations. From these studies it was found that *P. paradoxa* could be divided into three classes with respect to the various combinations of sterile spikelet types (see previous discussion) making up the inflorescence. These three inflorescence classes are as follows:

1. Clavate-reduced. This inflorescence class has "clavate" type sterile spikelets at the base which gradate into "reduced" type sterile spikelets at the tip. No "normal" type sterile spikelets are present. Represented by black bars in Figure 3.

2. Clavate-normal. Inflorescences of this class have "clavate" type sterile spikelets at the base and "normal" sterile spikelets near the tip. There are no "reduced" type sterile spikelets present. This class is represented by cross-hatched bars in Figure 3.

3. Clavate-reduced-normal. In this class of inflorescences there is a complete gradation from "clavate" sterile spikelets at the base to "reduced" sterile spikelets in the middle to "normal" sterile spikelets at the tip. This class is represented by unshaded bars in Figure 3.

The relationships between inflorescence length and inflorescence type are presented in Figure 3. In this figure, the horizontal axis is divided into seven equal size-classes representing inflorescence lengths. The vertical axis is calibrated to represent numbers of individuals.

Occasional intermediate inflorescence types occur: these have been arbitrarily placed in the class that they most nearly resembled.

As can be seen from Figure 3, clavate-reduced inflorescences are relatively short, mostly less than 5 cm in length. Clavate-normal inflorescence types are, on the average, slightly longer than the clavate

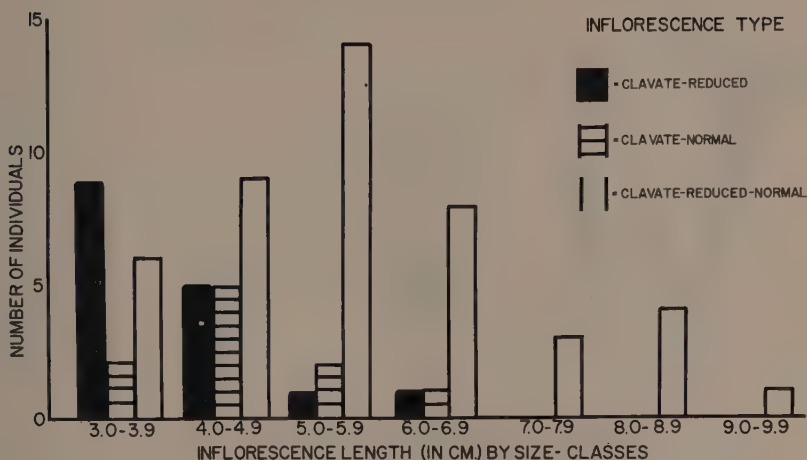


Figure 3. Relationship of inflorescence type to inflorescence length classes in Phalaris paradoxa.

reduced type. The third inflorescence type, clavate-reduced-normal, is found throughout the entire range of inflorescence-length values but occurs more commonly in the longer inflorescence size-classes.

None of the inflorescence-sterile spikelet relationships discussed above could be correlated with other features such as peduncle length, height of the mature plant, or geographic origin.

As can be gathered from the previously presented data, this species presents certain variation patterns. Various workers with the genus have given some of the extreme forms varietal or even specific distinction based upon one or more of the above-mentioned characters. When a large number of specimens are examined, it soon becomes apparent that, while the over-all variation patterns are such that vague sub-specific groups can be discerned, the overlap and merging of these variation patterns precludes any practical subdivision of the species.

Cytology and cytogenetics

Chromosome numbers of $2n=14$ have been reported for this species by Avdulov (1931), Miede (1939), Parthasarathy (1939), Hanson and Hill (1953) and Ambathsa (1956). The chromosome counts obtained by the author are presented in Table 3.

Cytological observations by the author showed meiosis to be regular in every respect. This corroborates the findings of Parthasarathy (1939).

Ostergren (1957) has experimentally produced autotetraploids ($2n=28$) in the self-fertile P. paradoxa by a pressurized nitrous oxide technique. No information concerning the morphology of the tetraploids was included.

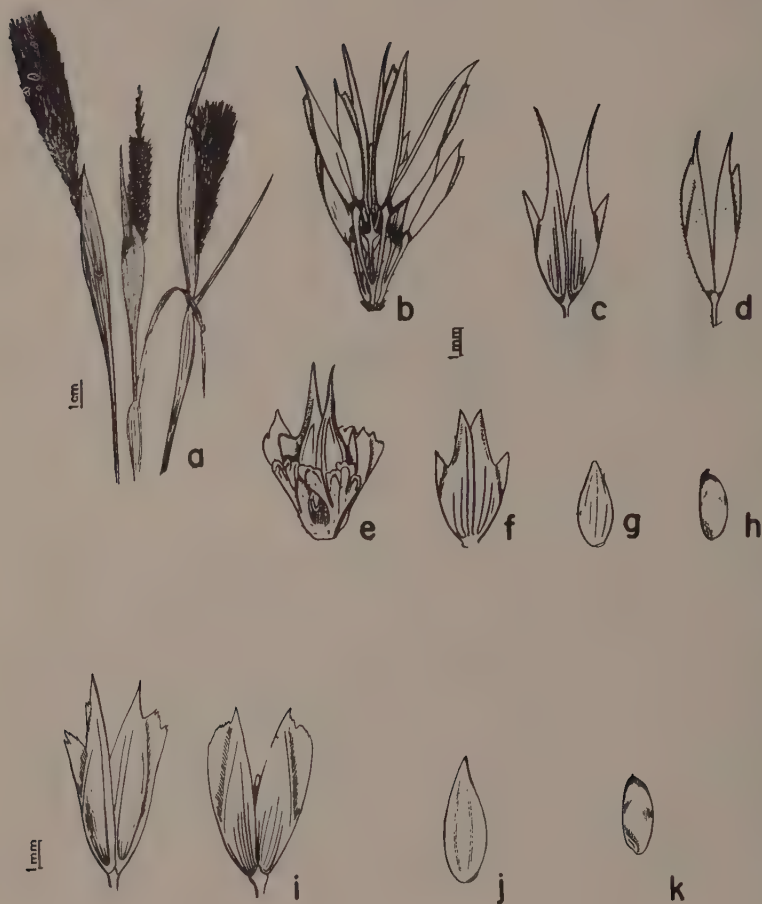


Plate 3. Phalaris paradoxa and Phalaris coerulescens.

a—h. Phalaris paradoxa; a. inflorescences, b. spikelet cluster with "normal" type sterile spikelet glumes, c. fertile spikelet from "b", d. sterile spikelet from "b", e. spikelet cluster with "clavate" type sterile spikelet glumes (in foreground) and "reduced" type sterile spikelet glumes in background, f. fertile spikelet of "e", g. fertile floret, h. caryopsis.

i—k. Phalaris coerulescens; i. spikelets, j. fertile floret, k. caryopsis.

Table 3. Chromosome numbers obtained from pollen mother cells of Phalaris paradoxa L..

Collection	Seed source location	Chromosome number
Plant introduction no. 170618 Anderson voucher no. 1201	Turkey	2n = 14

Distribution

Older floras list this species as being native to lands bordering on the Mediterranean Sea. Man's activities have extended the range throughout the world, primarily to harbor areas and waste places that have served as ballast or refuse dumps.

A map (Figure 4) shows the distribution of the specimens examined by the author.

Selected specimens examined

ALGERIA: Biskra, L. Chevallier 644 (US).

AUSTRIA: Gosting, F. Hopflinger, June 6, 1948 (US).

CANARY ISLANDS: Gomera, C.J. Pitard 389 (MO); Teneriffe, Parraudiara (F).

EGYPT: Cairo, G. Schweinfurth 1253 (US).

ENGLAND: Colchester, G.C. Brown, June 6, 1920 (US).

ETHIOPIA: Eritrea, Amasen, Dintori di Asmara, A. Pappi 6261 (MO, US).

FRANCE: Gentilly, rue de l'Hay, Jeanpert, June 28, 1919 (F).

GERMANY: Magdeburg, H. Eggert, July 6, 1861 (MO).

IRAQ: Baghdad, Y. Lazar 282 (F); Jebel Golat, H. Field and Y. Lazar 442 (F).

ISRAEL: Yokucan, A. Abraham, February 6, 1951 (MO).

ITALY: Corsica, Solenfora, P. Aellen 2908 (MO); Florence, A. Braun 1840 (MO).

JORDAN: Jenin, J.E. Dinsmore 4771b (F).

LIBYA: Tripoli, Post (US).

LEBANON: Bierut, Post, April 21, 1878 (US).

UNITED STATES: California: Butte Co., 7 miles west of Honcut, L.S. Rose 37381 (MO); Contra Costa Co., Byron Hot Springs, R.F. Hoover 2123 (US); Fresno Co., 9 miles southeast Dos Palos, H.L. Mason 12252 (US); Los Angeles, Sepulveda Blvd., L.C. Wheeler 1874 (F); San Diego, T.S. Brandegee, May, 1889 (F); Hawaiian Islands, Oahu, A.S. Hitchcock 13780 (US); Louisiana, New Orleans, W.T. Penfound, May 13, 1930 (US); Pennsylvania, Philadelphia, Ballast, J.C. Martindale, June, 1879 (US); Washington, Klickitat Co., Bingen, W.N. Suksdorf 5337 (US).

URUGUAY: Montevideo Dept., Punta Carretas, G. Herter 559 (US).

2. Phalaris coerulescens

Phalaris coerulescens Desf. Fl. Atl. 1:56. (1798) (Holotype in P)

Phalaris bulbosa Cav. Non L. Icon. Desc. Pl. 1:46. (1791)



Figure 4. Geographic distribution of Phalaris paradoxa.

Phalaris variegata Spreng. Neue Entdeck. 2:101. (1821)

Phalaris aquatica L. var. macrostachys Mutel. Fl. France. 4:15. (1837)

Phalaris villosula De Not. ex Parl. Fl. Ital. 1:73. (1848) pro syn.

Phalaris bulbosa L. var. nervosa Willk. in Willk. and Lange.

Prodr. Fl. Hisp. 1:37. (1861)

Phalaris coerulescens var. concolor Pojero. 3:251. (1908)

Phalaris bulbosa L. f. coerulescens (Desf.) Knoche. Fl. Balearica 1:289. (1921)

Phalaris paradoxa var. coerulescens (Desf.) Ruiz. Anal. Jard. Bot. Madrid. 8:486. (1947)

Description

Perennial; culms to 150 cm tall, bulbous at the base; panicle 3.0-11.6 cm long, 1.0-2.3 cm wide, usually cylindric, occasionally ovate-oblong; spikelets falling singly or in groups of 6 or 7, when falling in groups, 1 or 2 fertile and the rest staminate; glumes 5.3-9.0 mm long, 1.1-2.0 mm wide, glabrous or hirsute, winged, the wing up to 1.0 mm wide and markedly erose-denticulate; fertile floret 2.7-4.4 mm long; 0.7-1.4 mm wide, glabrous or with a very few short hairs on the margin of the lemma, shiny; sterile florets obsolete, often with a few short hairs at the base; grain 2.8-3.3 mm long, 1.2-1.4 mm wide, somewhat flattened; somatic chromosome number $2n=14$, the chromosome ca. 2.5-4.5 μ long at diakinesis.

Observations

Phalaris coerulescens is a robust perennial with well developed culm bases. The glabrous, lustrous fertile florets of this species serve to separate it from all other members of the genus except the annual species P. paradoxa.

P. coerulescens has somewhat larger spikelets and caryopses than P. paradoxa. A comparison of the two species with regard to these features is presented in Table 4.

Table 4. Comparison of Phalaris coerulescens Desf. and P. paradoxa L.

Character	<u>coerulescens</u>	<u>paradoxa</u>
Glume length	5.3-9.0 mm	5.5-8.2 mm
Fertile floret length	2.7-4.4 mm	2.5-3.5 mm
Caryopsis length	2.8-3.3 mm	2.3-2.6 mm
Caryopsis width	1.2-1.4 mm	0.9-1.1 mm

Referring to Table 4, it will be noted that there is an overlap in size ranges for all of the given structures except caryopsis size. The mature caryopses of P. coerulescens are somewhat larger than mature caryopses of P. paradoxa. While average size differences are apparent with respect to glume length and fertile floret length, the overlap of size ranges is enough to preclude their use as a practical means of separating the species.

An unusual characteristic possessed by P. paradoxa and some individuals of P. coerulescens is that the spikelets often fall in groups when ripe. In P. paradoxa the spikelets fall in groups of 7 (occasionally 6) with 6 (or 5) sterile spikelets surrounding the single fertile spikelet. The sterile spikelets are often deformed and reduced in size (Plate 3, b-f) and the florets contain only the aborted remains of the essential flower parts. Spikelets of P. coerulescens may fall singly or in groups. The number of spikelets in the groups varies from 5 to 8. Each group may have one or two fertile spikelets; the remaining spikelets are often staminate, although occasionally the flower parts are aborted. The sterile or staminate spikelets of P. coerulescens are never deformed and clavate (Plate 3, i, j).

Cytology and cytogenetics

Trumble (1935), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Hutton (1953), and Ambathsa (1956) report chromosome numbers of $2n=14$ for this species. Miede (1939) reports a $2n$ number of 28. Chromosome numbers obtained by the author are reported in Table 5.

Hayman (1956) reported P. coerulescens to be self-sterile. This self-sterility is supposedly under the control of two gene loci, each of which has a series of multiple alleles.

Nomenclature

A fragment of the holotype of P. coerulescens Desf. from the Muséum d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, France was examined by the author. Plate 3, i-k is drawn from the holotype material.

Distribution

A map (Figure 5) indicates the geographic origin of the specimens studied.

Table 5. Chromosome counts from pollen mother cells of Phalaris coeruleascens Desf.

Collection	Seed source: location	Chromosome number
Plant Introduction no. 240176 Anderson voucher no. 1224	Algeria	2n=14
Plant Introduction no. 240178 Anderson voucher no. 1226	Algeria	2n=14
Plant Introduction no. 240179 Anderson voucher no. 1225	Algeria	2n=14
Plant Introduction no. 240188 Anderson voucher no. 1179	Algeria	2n=14
Plant Introduction no. 240189 Anderson voucher no. 1220	Portugal	2n=14
Plant Introduction no. 240190 Anderson voucher no. 1175	Portugal	2n=14

Selected specimens examined

CANARY ISLANDS: Gomera, San Sebastian, J. Bornmuller 2922 (MO); Gran Canaria, Santa Brigida, A.C. Cook 638 (F, MO).

GIBRALTAR: Munro 1854 (MO).

GREECE: Crete, La Canee, Lieur humides, E. Reverchon, May 29, 1883 (US); Karpatos Isl. Lasto 649 (US).

ITALY: Corsica, sari de Portorecchio, P. Aellen 2906 (MO); Naples (US); Pisa, H. Van Heurck 1868 (F); Rome, Bereuger, April, 1882 (US); Sicily, Palermo, Todaro 1071 (US).

PORTUGAL: Madeira Isl., river near Funchal (US); Herdade do monte das aldeias pr. Estremoz, A. Fernandes 1639 (MO).

SPAIN: Grenada Prov., Barranco del Rio Segura, prairies humides sur le calcaire, E. Reverchon 1299 (US); Majorca Isl., Barranco de Solter, E. Bourgeau 2811 (US); Malaga, Estepona, Ellmand and Nelmes 163 (US).

3. Phalaris minor

Phalaris minor Retz. Fasc. Obs. Bot. 8 (1783)

Phalaris decumbens Moench. Meth. Pl. 208 (1794)

Phalaris aquatica var. minor (Retz.) Mutel. Fl. Franc. 4:15. (1837)

(Based on Phalaris minor Retz.)

Phalaris nepalensis Trin. Sp. Gram. Icon. Descr. 1:80. (1828)

(Holotype in LE)

Phalaris brevis Ehrenb. ex Trin. Mem. Acad. St.-Petersb. Ser. 6.

5:50. (1840) (Holotype in LE)

Phalaris trivialis Ehrenb. ex Trin. Mem. Acad. St.-Petersb. Ser. 6.

5:50. (1840)



Figure 5. Geographic distribution of Phalaris coerulescens and P. truncata.

Phalaris gracilis Parl. Pl. Nov. 36. (1842)

Phalaris minor var. gracilis (Parl.) Parl. Fl. Ital. 1:70. (1848)

(Based on P. gracilis Parl.)

Phalaris ambigua Fig. and De Not. Mem. Acc. Torin. 14:10. (1853)

Phalaris minor var. hematites Duval-Jouve and Paris in Paris, Bull. Soc. Bot. Fr. 14:276. (1867)

Phalaris minor var. integra Trab. Bull. Soc. Bot. Fr. Ser. 2. 7:394. (1885)

Phalaris minor var. comulosa Heldr. Bull. Herb. Boiss. 4:396. (1898)

Phalaris minor var. bracheata Jans. and Wacht. Nederl. Kruidk. Archief 6:132. (1916)

Phalaris minor var. composita Jans. and Wacht. Nederl. Kruidk. Archief. 6:132. (1916)

Phalaris minor var. glomerata Henr. ex Jans. and Wacht. Nederl. Kruidk. Archief. 6:132. (1916)

Phalaris minor f. subcylindrica Web. and Thell. ex Jans and Wacht. Nederl. Kruidk. Archief. 6:132. (1916)

Phalaris minor var. integra Trab. f. phaenosperma Cavara. Bull. Dell'Orto Bot. Nap. 9:42. (1928)

Phalaris arundinacea ssp. bulbosa Ruiz var. minor (Retz.) Ruiz. Anal. Jard. Bot. Madrid. 8:489. (1947) (Based on Phalaris minor Retz.)

Phalaris minor f. hematites (Duval-Jouve and Paris) Maire. Fl. Afr. Nord. 23. (1953)

Description

Annual; stems 20-100 cm tall; panicle ovate-oblong, 1-6 cm long, 1-2 cm wide; glumes 4.0-6.5 mm long, more or less equal, keel broadened into a conspicuous wing near the tip, the wing usually erose-denticulate, occasionally entire; fertile lemma 2.7-4.0 mm long, 1.2-1.8 mm wide, usually broadly lanceolate-ovate, dull yellow when immature, gray-brown and shiny at maturity, pubescent; sterile floret 1, 1.0-1.8 mm long or very short, only 0.2-0.3 mm long; grain 2.3-2.5 mm long, 1.3-1.5 mm broad, somewhat flattened; chromosome number 28 or 29, the chromosomes ca. 3-7 μ long.

Observations

Phalaris minor is an annual grass presently of world-wide distribution. Taxonomically the species is quite uniform except for a form with short sterile florets (Plate 4, d, e) which occurs in India and Afghanistan. This was named Phalaris nepalensis by Trinius in 1828. Twelve years later he named this same form P. brevis. This form differs from P. minor only in that it has a very much reduced sterile floret which is never more than 0.3 mm long. Neither form differs from the other in features such as glume shape, lemma shape, inflorescence size and shape, stature of plants, etc. Since these two taxa are distinct only as to size of sterile florets and are identical in other morphological features, the author feels there is not enough difference to warrant nomenclatorial recognition.

Ruiz (1947) reduced P. minor to the status of a variety as P. arundinacea ssp. bulbosa Ruiz var. minor (Retz.) Ruiz. P. arundinacea differs from P. minor in a number of features. These are enumerated below:

1. P. arundinacea is a large, robust, rhizomatous perennial while P. minor is a rather weak, fibrous-rooted annual.

2. The glumes of P. arundinacea are rarely winged; if wings are present, they are very narrow and barely visible under 10X magnification. The glumes of P. minor are broadly winged; the wings are easily visible under 10X magnification.

3. P. arundinacea has two well-defined sterile florets; P. minor has only one sterile floret.

4. The fertile florets of P. arundinacea are relatively narrow while those of P. minor are much broader by comparison. Fertile florets of P. arundinacea are more or less circular in cross-section outline; those of P. minor are distinctly flattened in this respect.

Cytology and cytogenetics

Chromosome numbers of $2n=28$ have been reported for this species by Avdulov (1931), Parthasarathy (1939), Hanson and Hill (1953), Hutton (1953), and Ambathsa (1956). Counts of $2n=29$ have been reported by Hanson and Hill (1953). Chromosome counts obtained by the author are reported in Table 6.

Parthasarathy (1939) states that occasional quadrivalents are recognizable in side views of metaphase figures in P. minor. This would seem to be evidence that homologous segments are present.

Observations of greenhouse-grown material by the author revealed a number of interesting and puzzling meiotic aberrations (Plate 4, f-h).

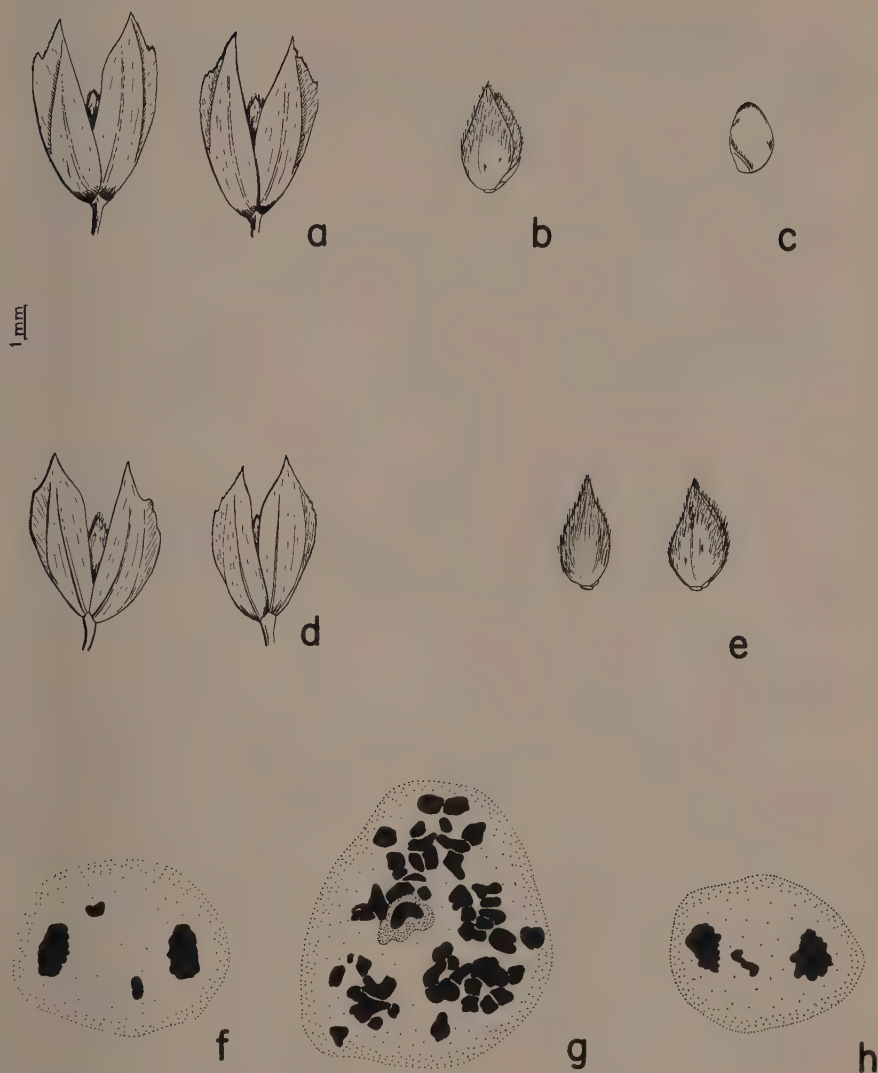


Plate 4. Phalaris minor

- a. spikelets,
- b. floret,
- c. caryopsis,
- d. spikelets from holotype of Phalaris nepalensis,
- e. florets from holotype of P. nepalensis,
- f-h. aberrant meioses,

Table 6. Chromosome numbers from pollen mother cells of Phalaris minor Retz.

Collection	Seed source location	Chromosome number
Plant Introduction no. 208404 Anderson voucher nos. 1178, 1190	Transvaal	2n=28, 29 (1178) 2n=28 (1190)
Plant Introduction no. 202678 Anderson voucher no. 1174	unknown	2n=28
Plant Introduction no. 180865 Anderson voucher no. 1187	Turkey	2n=28
Plant Introduction no. 211064 Anderson voucher no. 1200	Afghanistan	2n=28

Many metaphase I, anaphase I, and telophase I cells showed lagging chromosomes (Plate 4, f, h). Quadrivalent formation was observed with some degree of frequency. Occasional fragments and lagging bivalents could be seen. Positive counts were difficult to make because of the tendency for the bivalents to stick together in groups, refusing to separate without mutilation of the cell. It is possible that some or all of the observed abnormalities in the author's material may have been due to greenhouse conditions.

Three hybrids have been obtained in crosses involving P. minor as the male parent. Trumble (1935) and Hutton (1953) obtained crosses between the annual, self-compatible P. minor (2n=28) and the perennial, self-sterile P. coerulescens (2n=14). The resulting F₁ hybrid was vigorous but completely sterile. Hutton also used a colchicine technique to produce an allopolyploid (2n=42) between these two species. These were annuals and tended to be less vigorous than either parent. Hutton noted a dominance of P. minor characters in this hybrid and attributes this to the fact that P. minor contributed two-thirds of the chromosomes in the hybrid genome.

Hayman (1955) studied the meiotic behavior of the hybrid reported by Hutton and found that it formed seven bivalents and seven univalents during meiosis. The seven univalents belonged to the P. minor set of chromosomes and showed several kinds of chromosomal aberrations such as short inversions, multiple armed chromosomes, and breakages. Hayman claimed that a considerable degree of homology existed in the pairs of bivalents because of relatively high mean chiasma frequency.

Hybrids between P. minor and P. aquatica are reported by Trumble (1935) and Hutton (1953). Hutton reported the resulting F₁ to be sterile. Hayman (1955), in studying Hutton's hybrid material, found that linear trivalents occurred in ninety per cent of the cells and that there were between eight and nine univalents, on the average, per cell. Blake (1956) reported that Hutton's allopolyploid showed considerable promise as a

forage grass in Australia and named it X Phalaris daviesii. According to Blake this taxon is cultivated and has not escaped.

Trumble (1935) obtained hybrids by crossing P. minor and P. arundinacea. Ambathsa (1956) studied these plants cytologically and reported that they produced a good proportion of normal pollen grains but were highly sterile.

Nomenclature

The type species of Phalaris minor Retz. was not seen. Retzius' original description is quite complete and leaves no doubt as to the typification of the species.

The holotypes of both P. nepalensis and P. brevis are in the Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the U.S.S.R., Leningrad and were examined by the author. Drawings of spikelets from the holotype of P. nepalensis are presented in Plate 4, d, e.

Distribution

The range of P. minor is world-wide at the present time. The original range, as given in older floristic treatments, appeared to be roughly the area bordering upon the Mediterranean Sea. In more recent years specimens have been collected from waste areas (harbor ballast, refuse dumps, etc.) throughout much of the rest of the world.

A map (Figure 6) shows the geographic origin of the specimens studied by the author.

Selected specimens examined

AFGHANISTAN: Shibarghan, A.T. Semple 409 (US); Griffith 6468 (MO).

ALGERIA: Sidi-bel-Abbes, A. Warioux, April 28, 1873 (US).

ANGOLA: Mossamedes, Huilla, Gossweiler 9419 (US).

AUSTRALIA: Tasmania, Campbelltown, R.A. Black 1183.007 (US); West Australia, Perth, R. Helms H.140 (US).

AUSTRIA: Tergestem, Noe (MO).

AZORES ISLANDS: Sta. Maria, Correiro 867a (MO).

BRAZIL: Sao Paulo, Seccaco, Villa Cerqueira Cesar, F.C. Hoehne 4658 (US).

CANARY ISLANDS: Teneriffe, C. Bolle, 1856 (MO).

COLOMBIA: Bogota, Bros. Appollinaire, Arthur 22 (US); Boyaca Dept., vic. Cocuy, J. Cuatrecasas 1697 (F, US).

EGYPT: Alexandria, J. Bornmuller 11037 (US); Cairo, J. Bornmuller 11038 (US).

ENGLAND: Jersey, Georgetown, L.V. Lester, July 9, 1897 (F).

FRANCE: Cherbourg, L. Corbiere, July 22, 1886 (US); Paris, Villeneuve le Roi, Jeanpert, May 13, 1920 (F).

GERMANY: Magdeburg, H. Eggert, June 1868 (MO).

GREECE: Aegina Isl., T. de Heldreich and T. Holzmann, April 18-26, 1881 (US); Karpatos Isl., W. Barbey 647 (US); Kastrades Isl., C. Baenitz, May 5, 1896 (US).

INDIA: Jhelum Dist., Hirnpur, K.L. Malhotra 15841a (US); Punjab, Bhadwar, Kangara, W. Koelz 4178 (US); United Prov., Dehra Dun, Balupur, U. Singh 314 (F); Kapkot, W. Koelz 20052 (US); Rawalpindi, garden weed, R.R. Stewart 17285a (US).



Figure 6. Geographic distribution of Phalaris minor.

IRAN: Yesd Prov., J. Bornmuller 4821 (US); pr. Gere inter Abuschir et Schivas, T. Kotschy 88 (MO).

IRAQ: Arbil Prov., M. al Radle 3866 (US); Nasirujah, near Baghdad, Y. Lazar, March 23, 1935 (F).

ITALY: Leghorn, Livorno, Philippi, 1888 (US); Sardinia, Santa Teresa Gallure, E. Reverchon 148 (US); Sicily, Syracuse, G. Rigo 13 (US).

MADEIRA ISLANDS: W. Trelease, June 15, 1896 (MO).

MEXICO: Baja California, Tia Juana, I.L. Wiggins 5105 (US); Puebla, Puebla, Bros. Arsene and Nichols 5725 (MO).

PERU: Lima, Miraflores, A.S. Hitchcock 22346 (US).

PORTUGAL: Coimbra, M. Ferreira 617 (US); Lisbon, Estremadura, Serra de Monsanto, A.R. da Cunha, 1888 (US); Serra d'Orre, Herdade da Querijeira, A. Fernandes 1737 (MO).

SPAIN: Seville, Baetins, M. Gandoger, 1906 (MO).

SAUDI ARABIA: Chappa, W. Schimper 247 (US).

TUNISIA: Sfax, Espina, 1854 (F).

TURKEY: Smyrna, J. Bornmuller 10108 (US).

UNION OF SOUTH AFRICA: Cape of Good Hope, 12 miles north of Piquetburg, abundant in cultivated fields, R.K. Godfrey SH-1251 (US); Johannesburg, C.E. Moss 13556 (US).

UNITED STATES: Arizona: Pima Co., 15 miles west of Tucson, annual weed, K.F. Parker 8018 (US); Pinal Co., Casa Grande, K.F. Parker 8243 (US); California: Alameda Co., Berkeley, W.C. Blasdale, June 22, 1895 (US); Colusa Co., 4 miles east of Williams, R.S. Ferris 508 (MO); San Bernardino Co., south of Chino, P.A. Munz 15573 (US); San Diego Co., Nestor, H.P. Chandler 5118 (US); San Mateo Co., Crystal Springs Lake, A.D.E. Elmer 4427 (MO); Santa Barbara Co., Gaviota, A. Chase 5639 (US); Stanislaus Co., 4 miles west of Hoover, R.F. Hoover 1230 (US); Catalina Island, L.W. Nuttall 224 (US); Florida: Lake City, A.W. Bittung 778 (MO, US); Hawaiian Islands, Oahu, Schofield Barracks, A.S. Hitchcock 13915 (US).

URUGUAY: Soriano, escaped from cultivation, Gallinal PE-5379 (US).

4. Phalaris arundinacea

Phalaris arundinacea L. Sp. Pl. 55. (1753) (Holotype in LINN;
photograph of type specimen in GH)

Phalaris arundinacea L. var. picta L. Sp. Pl. 55. (1753) (Holotype
in LINN; photograph of type specimen in GH)

Arundo colorata Aiton. Hort. Kew. 1:116. (1789) (Based on
P. arundinacea L.)

Typhoides arundinacea (L.) Moench. Meth. Pl. 202. (1794)

Calamagrostis colorata (Ait.) Sibth. Fl. Oxon. 37. (1794) (Based on
Arundo colorata Ait.)

Arundo riparia Salisb. Prodr. Stirp. 24. (1796) (Based on
P. arundinacea L.)

Calamagrostis variegata With. Bot. Arr. Veg. Brit. ed.3. 2:124.
(1796)

Baldingera colorata Gaertn., Mey., and Scherb. Fl. Wett. 1:96.
(1799)

Diagraphis arundinacea (L.) Trin. Fund. Agrost. 127. (1820)

Baldingera arundinacea (L.) Dum. Obs. Gram. Belg. 130. (1823)

Phalaris arundinacea var. ramosa Gaudin. Fl. Helv. 1:160. (1828)

Phalaris arundinacea var. colorata Hartm. Hanb. Skand. Fl. ed.4.
22. (1843)

Phalaris arundinacea var. variegata Parnell. Grasses Brit. 188.
(1845)

Phalaris japonica Steud. Syn. Pl. Glum. 1:11. (1855) (Holotype in L)

Baldingera arundinacea var. picta (L.) Nyman. Consp. Fl. Eur. 791.
(1878)

Phalaridantha arundinacea (L.) Cariot. Etude des Fl. 900. (1889)

Phalaris arundinacea var. thyreoides Willk. Oesterr. Bot. Zeitsch.
40:145. (1890)

Phalaris arundinacea f. pallida Schwarz. Flor. Nurn-Erlang. 855.
(1892)

Endallex arundinacea Raf. ex Jacks. Ind. Kew. 1:839. (1893) pro syn.

Phalaris hispanica de Coincy. Morot. Journ. de Bot. 8:207. (1894)

Phalaris arundinacea f. luteo-picta Voss in Siebert and Voss.
Vilmorin's Blumengart. 1198. (1896)

Phalaris arundinacea f. picta (L.) Asch. and Graebn. Syn. Mitt. Eur.
Fl. 24. (1898)

Baldingera arundinacea (L.) Dum. var. rotgesii Husnot. Gram. (1899)

Phalaris arundinacea var. genuina Hack. Bull. Herb. Boiss. 7:646.
(1899)

Phalaris arundinacea var. japonica (Steud.) Hack. Bull. Herb. Boiss.
7:646. (1899)

Phalaris arundinacea f. ramifera Junge. Hamb. Wiss. Anst. 22:60.
(1905)

Phalaris arundinacea f. pallens Stebler ex Hegi. Fl. Mitt. Eur.
1:197. (1906)

Phalaris arundinacea ssp. ochleri Pilger. Bot. Jahrb. 43:91. (1909)

Phalaris arundinacea f. minor Jans. and Wacht. Nederl. Kruidk.
Archief. 6:141. (1916) (Not P. minor Retz.)

Phalaris arundinacea race P. rotgesii (Husnot) Letard. ex Jans. and
Wacht. Nederl. Kruidk. Archief. 6:142. (1916)

- Phalaris arundinacea var. genuina Maire non Hackel. Bull. Soc. Hist. Nat. Afr. 32:217. (1953)
- Phalaris arundinacea var. leioclada Maire. Bull. Soc. Hist. Nat. Afr. Nord. 32:217. (1941)
- Phalaris arundinacea ssp. typica Ruiz. Anal. Jard. Bot. Madrid. 8:489. (1947)
- Phalaris arundinacea ssp. typica Ruiz f. picta (L.) Ruiz. Anal. Jard. Bot. Madrid. 8:489. (1947)
- Phalaris arundinacea ssp. typica Ruiz f. thyrsoides (Willk.) Ruiz. Anal. Jard. Bot. Madrid. 8:489. (1947)
- Phalaris arundinacea var. latifolia Henr. ex Jans. Fl. Neerl. 243. (1951)

Description

Perennial from scaly, creeping rhizomes; culms 50-150 cm tall; leaves usually green, occasionally striped with white (in f. picta); panicle 7-40 cm long, lobed and branched at the base, the branches up to 5 cm long, spreading during anthesis; glumes 3.5-7.5 mm long, more or less equal, acute, usually wingless, when winged, the wing very narrow and inconspicuous, keel scabrous; fertile floret 2.7-4.5 mm long, lanceolate, dull yellow when immature, gray-brown and shiny at maturity, nerves conspicuous, glabrous or with a few appressed scattered hairs; sterile florets 2, 1.2-2.3 mm long; subulate, pubescent; grain 1.5-2.0 mm long, 0.7-1.0 mm wide, subovoid brown with faintly striate surface; somatic chromosome number 14, 27, 28, 29, 30, 31, 35, or 42; the chromosomes ca. 5.0 μ long at diakinesis.

Observations

Phalaris arundinacea L., commonly called Reed Canary Grass, is a well-defined though highly variable species. The most distinct variant within the species is P. arundinacea f. picta (L.) Asch. and Graebn. commonly called "Ribbon Grass" or "Gardener's Garters." This form differs from the typical in having its leaves longitudinally striped with yellow-white achlorophyllous strips. The spikelets of f. picta do not differ noticeably from those of f. arundinacea in general shape but they do tend to be somewhat smaller in size. The author did not see any mature caryopses on any living or dried specimen of Ribbon Grass examined. The absence of mature fruits might be attributed to the aberrant meiosis that has been reported for this form (Church, 1929). Church reported that pollen in f. picta was 30-40% imperfect. Diakinesis and metaphase I revealed 15 bivalents and one or two univalents which consistently lagged on the spindle. The lagging univalents, as well as some of the bivalents, were extruded and disintegrated. More work on the cytology and genetics of this form are needed in order to learn more about the abnormalities in meiotic behavior.

Almost all collections of f. picta seen by the author were from cultivated stands. Escaped populations are sometimes found near dwellings. The author has never observed any plants of this form in a naturally occurring population of f. arundinacea.

The nonstriped populations of Phalaris arundinacea have been divided into no less than ten infraspecific categories, including varieties, sub-

species, formae, and races. Many of the described infraspecific taxa were based upon vegetative characters such as the amount of branching, leaf coloration, and size, shape, and density of the inflorescence.

Baltensperger and Kalton (1958) analyzed several vegetative characters of reed canary grass from an agronomic standpoint. Plant materials used in their study were obtained from 37 seed lots collected in the United States and one each from Turkey and Canada. These seeds were grown in field plots. Their results are useful taxonomically in showing some of the variation patterns within the species. The range in leaf width was from 9 to 25 mm. The total variability in forage value was quite high; much of this variability was attributed to environmental effects.

Field observations by the present author indicated considerable variability in height at anthesis, size and shape of the inflorescence, and over-all coloration depending upon the habitat of the plants. Within a single clone, as much as one meter difference in height of flowering culms was observed. The panicle size and shape varies a great deal depending upon the stage of development. None of these variations could be correlated with one another or with geographic distribution to indicate subspecific populations.

The perennial, prominent scaly rhizomes, lobed or branched panicle, acute, almost wingless glumes, lustrous, narrow, sparsely pubescent lemmas, and two villous sterile florets distinguish this species from others of the genus.

Cytology and cytogenetics

Numerous cytological studies have been made upon members of this species. These studies indicate that at least some members of the taxon are aneuploids. Aneuploid numbers of $2n=27$, 29, 30 and 31, have been reported by Hanson and Hill (1953). Euploid numbers of $2n=14$ were reported by Church (1929); $2n=28$ by Church (1929), Avdulov (1931), Jenkin and Sethi (1932), Trumble (1935), Parthasarathy (1939), Hutton (1953), Tateoka (1954), Carnahan and Hill (1956), and Ambathsa (1956); $2n=35$ by Hanson and Hill (1953); $2n=42$ by Brock (unpublished, listed in Darlington and Wylie, 1955). Carnahan and Hill (1956) experimentally produced plants with $2n=56$. The author's observations and those of the above workers indicate that meiosis seems quite regular in the euploid collections. The aneuploid sections show, as would be expected, various meiotic irregularities (Hanson and Hill, 1953).

To the author's knowledge, no one has attempted a comparison of chromosome number and various other characters such as panicle size, degree of lobing, spikelet size, etc. Until such studies are made, one can only speculate that perhaps some of the rather broad range of variability can be attributed to differences in ploidy.

The meiotic chromosome number obtained by the author is presented in Table 7.

Nomenclature

Photographs (in GH) of the holotypes of both Phalaris arundinacea var. arundinacea and var. picta (in LINN) were examined. These represent the taxa as commonly understood today.

Britton and Brown (1913) designated P. arundinacea as the type species of the genus.

Table 7. Chromosome number from mother cells of Phalaris arundinacea L. f. arundinacea

Collection	Location	Chromosome number
Anderson voucher no. 1235	Iowa, Story Co.	2n=28

Distribution

Members of this species have been found almost throughout the northern hemisphere and, as introductions, on all of the continents in the southern hemisphere except Antarctica. Large colonies are often found in the northern United States, most frequently in roadside ditches, along pond margins, dredge ditches, and creek banks.

A map (Figure 7) shows the geographic origin of the specimens studied by the author.



Figure 7. Geographic distribution of Phalaris arundinacea.

Selected specimens examined

Phalaris arundinacea f. arundinacea. CANADA: Alberta, Calgary, A.S. Hitchcock 4985 (US); Alberta, Slave Lake, E.H. Moss 6062 (GH); British Columbia, Vancouver Isl., W.R. Carter 934 (GH); New Brunswick: Cambelltown, R. Chambers 29253 (F, US); Newfoundland: Exploits River, Grand Falls, M.L. Fernald, K.M. Wiegand 4526 (F, US); Humber Distr., Serpentine Lake, E. Rouleau 2386 (US); Northwest Territories, south of Fort Smith, 60°0.2'N, 112°38'W, W.J. Cody and C.C. Loan 4683 (NDA); Nova Scotia, Cape Breton Isl., G.E. Nichols 943 (GH); Ontario: Algoma Dist., Corbeil Pt., 47°00'N, 84°45'W, T.M.C. Taylor 1104 (GH, US); Bruce Co., Red Bay, G.L. Stebbins 27 (GH); North Shore, Schreiber, 48°45'N, 87°15'W, R.C. Hosie 1321 (GH); Quebec: Anticosti, J. Macoun 29254 (US); Gaspé Peninsula, 4 miles above mouth of Bonaventure River, W.G. Dore 47-923 (US); Saskatchewan, Grand Trunk

Pacific RR., 20 miles west of Yorkton, J. Macoun and W. Herriot, July 9, 1906 (F, US).

CEYLON: top of Adam's Peak, introduced, A.H.G. Alston 950 (US).

CHINA: Chihli Prov., Peitaiho, M.S. Clemens 7005 (US); Kiansu Prov., Nanking, A.N. Steward 2528 (US); Shansi Prov., Ning-wu Hsien, 7000' elev., T. Tang 1444 (US); Szechuan, Sung-pan Hsien, W.P. Feng 4401 (US).

COLOMBIA: Sopo, 2640 m. elev., Bros. Apollinaire and Arthur 23 (US).

ENGLAND: Lancashire: Lake Windermere, near High Wray, M.R. F. Taylor 3 (US); Mersey, Speke, A.E. Lomax (US); Middlesex, Chiswick, Stand-on-the-Green, F. Ballard 138 (US).

FRANCE: Allier-Yeure, Robe, S.E. Lassimonne, June, 1894 (US).

GERMANY: Nurnberg, F. Eberleu and L. Gross 192 (US); Rheinpfak, Durkheim, H. Gluck, July, 1932 (US).

HUNGARY: Haidu-Puspok-Ladany, A. de Degen 54 (US).

IRAN: Azna, M. Koie, June 8, 1937 (GH); Urmia, 13 miles north, Cowan and Darlington 1500 (US).

ISRAEL: Tel-Aviv, Eig, June 26, 1928 (US).

ITALY: Helvajujana, Padule di Castagnolo (F).

JAPAN: Mino Prov., Hondo, K. Shiota 5219 (GH); Miyazaki Prov., Miyazaki City, Kitakata, N. Eri 100575 (GH).

JAVA: Diegnplatcan, Backer 21702 (US).

KOREA: Seoul, Kyengki, R.K. Smith (GH).

MANCHURIA: Jalactun, Dorsett and Dorsett 3500 (US).

MEXICO: Valle de Mexico, Santa Anita, Fournier 148 (GH).

NORWAY: Nordland fylke, Berthesi Bodin, Andr. Noto, May 5, 1922 (GH).

PORTUGAL: Coimbra, Choipal, A. Moller, June, 1886 (US).

ROMANIA: Turda Dist., Borza and Bujorean 724 (US).

SWEDEN: Hedemora, Dalarne, G.A. Ringselle 18-290 (GH).

SWITZERLAND: Basel, C. Christ (US); Zurich, F.G. Stebler and C. Schroter, May 8, 1887 (US).

UNION OF SOUTH AFRICA: Pretoria, Ladybraud, A.P. Rousseau 1042 (US).

UNION OF SOVIET SOCIALIST REPUBLICS: Kamtchatka, Savoiko-Petropavlovsk, E. Hulten, July 26, 1928 (US); Siberia: Kudia River, J.D.A. Cockerell, July, 1923 (US); Tobolsk, Mameev 877 (US).

UNITED STATES: Alaska, Manley Hot Springs, near Tanana R., E. Scamman 3663 (GH); Arizona, Crater Lake, T. McDougal 334 (US); California, San Joaquin Co., Stockton, E.E. Stanford 190 (US); Warner Mts., D. Griffiths and B. Hunter 407 (US); Colorado: Gunnison Co., Gunnison, C.L. Shear 939 (GH, US); Routt Co., Yampa, Shear and Bessey 1416 (US); Connecticut, Franklin, R.W. Woodward, July 20, 1900 (GH); Delaware, New Castle Co., Talleyville, R.R. Tatnall 4273 (GH); District of Columbia, Washington, G. Vasey, June, 1884 (US); Idaho, St. Anthony, E.D. Merrill and E.N. Wilcox 135 (US); Illinois: Stark Co., Spoon River, V.H. Chase, June 16, 1900 (F, US); Union Co., J.W. Thieret 3200 (F); Indiana: Bartholomew Co., 1 mile east Oglesville, C.C. Deam 34274 (US); Marion Co., Indianapolis, R.C. Friesner 16935 (GH); Iowa, Emmet Co., A. Hayden 48 (ISC); Kansas, Meade Co.,

2 miles north of Fowler, W.H. Horr 3550 (GH, US); Maine, Aroostook Co., Van Buren, M.L. Fernald 167 (GH, US); Maryland, Garrett Co., J.D. Smith, June, 1879 (US); Massachusetts, Berkshire Co., North Adams, M.L. Fernald and B. Long 8688 (GH); Michigan, Cheboygan Co., Douglas Lake, J.H. Ehlers 549 (GH, US); Minnesota, Big Stone Co., Ortonville, P. Johnson 394 (GH); Missouri, Linn Co., J.A. Steyermark 40427 (F, GH); Montana, Madison Co., Cliff Lake, P.A. Rydberg and E. A. Bessey 3548 (GH, US); Nebraska, Grant Co., 3 miles n.e. of Whitman, P.A. Rydberg 1621 (GH, US); Nevada, Battle Mtn., A.S. Hitchcock 10599 (US); New Hampshire, Coos Co., Colombia, A.H. Moore 3854 (GH); New Jersey, Hunterdon Co., Annandale, H.L. Fisher, June 25, 1914 (US); New Mexico, Rio Arriba Co., Chama, P.C. Standley 6806 (US); New York, Cayuga Co., Conquest, A.J. Eames and F.P. Metcalf 5593 (GH); North Carolina, Jackson Co., Balsam, H.L. Blomquist 9772 (GH); North Dakota, Ramsey Co., Church's Ferry, M.A. Brannon 59, (US); Ohio, Champaign Co., Chapman's Creek, E.C. Leonard 415 (US); Oregon, Douglas Co., Diamond Lake, F.V. Coville and E.I. Applegate 474 (US); Pennsylvania, Elk Co., Silcox, H.A. Wahl 766a (GH); South Dakota, Aurora Co., E.N. Wilcox 38 (US); Utah, Provo Canyon, Sereno Watson 1347 (GH, US); Vermont, Manchester, M.A. Day 211 (GH, US); Virginia, Arlington Co., Clarendon, H.A. Allard 2976 (GH); Washington, Douglas Co., Sandberg and Leiberger 330, June 1893 (US); West Virginia, Tucker Co., Canaan Valley, H.A. Allard 9190 (GH, US); Wisconsin, Dane Co., 20 miles east of Madison, R.E. Shake 247 (NDA); Wyoming, Carbon Co., Grand Encampment, Aven Nelson 3987 (GH, US).

Phalaris arundinacea f. *picta*. CANADA: Nova Scotia, Yarmouth Co., A.S. Pease and B. Long 19856 (GH); Ontario, Ottawa Dist., Ottawa, J. M. Gillett and W.G. Dore 1489 (US); Quebec, Boucherville, M. Victorin and R. Germain 49344 (GH).

ECUADOR: Tungurahua Prov., Ambato, garden, 2550 m. elevation, M.S. Solis 9399 (US).

EL SALVADOR: Volcan de San Salvador, in garden, P.C. Standley 22860 (US).

GUATEMALA: Jalapa, 1360 m elev., P.C. Stanley 76364 (F).

JAPAN: Shikoku, U. Faurie 4465 (US).

UNITED STATES: Illinois, Cook Co., J.W. Thieret 1398 (F); Indiana, Pine Co., Lake Chicago Basin, C.W. Duesner 1908 (F); Iowa, Calhoun Co., Lohrville, D. McClure 317a (ISC); Maine, Westbrook, P.L. Ricker 659 (US); Massachusetts, Greenfield, E.F. Williams, June 17, 1910 (GH); Michigan, Keeweenaw Co., Copper Falls, F.J. Hermann 7762 (US); Missouri, Garrett Co., Oakland, J.D. Smith, July 1879 (US); New Hampshire, Laconia, garden, L.A. Carter 236 (US); New York, N. Hannibal, O.E. Pearce, July 16, 1883 (US); Ohio, Coshocton Co., Coshocton, H.N. Moldenke 12970 (US); Rhode Island, Newport Co., M. L. Fernald, B. Long, and G.S. Torrey 8689 (GH); Vermont, Peacham, A.F. Stevens, 1892 (US); Wisconsin, Sturgeon Bay, J.H. Schuette, July 12, 1885 (F).

5. Phalaris aquatica

Phalaris aquatica L. Amoen, Acad. 4. 264. (1755) (Holotype in LINN. Photograph of holotype in GH)

Phalaris tuberosa L. Mant. Pl. 2:557. (1771) (Holotype in LINN. Photograph of holotype in GH)

Phalaris nodosa Murr. Syst. Veg. ed. 13. 88. (1774) (not P. nodosa L., presumably based on P. tuberosa L.)

Phalaris bulbosa var. hirtiglumis Batt. and Trab. Bull. Bot. Soc. Fr. 7:395. (1885)

Phalaris tuberosa var. alata Batt. and Trab. Fl. Alg. Monocot. 2:140. (1895)

Phalaris tuberosa var. hirtiglumis (Batt. and Trab.) Batt. and Trab. Fl. Alg. Monocot. 2:140. (1895) (Based on P. bulbosa var. hirtiglumis Trab.)

Phalaris nodosa var. minor Pojero. Fl. Sic. 3:251. (1908) (Not based on P. minor Retz.)

Phalaris stenoptera Hackel. Repert. Sp. Nov. 5:333. (1908)

Phalaris elongata Braun-Blanquet in Braun-Blanquet and Maire. Bull. Hist. Nat. Afr. Nord. 13:22. (1922) (Holotype in SIGMA)

Phalaris tuberosa var. clausonis Maire and Trabut in Maire. Bull. Soc. Nat. Afr. Nord. 24:230. (1933)

Phalaris tuberosa var. stenoptera (Hack.) Hitchc. Wash. Acad. Sci. Jour. 24:292. (1934) (Based on P. stenoptera Hack.)

Phalaris arundinacea ssp. bulbosa Ruiz. Anal. Jard. Bot. Madrid. 8:489. (1947) (Based on P. bulbosa L. as misapplied by Ruiz to P. aquatica L.)

Phalaris bulbosa var. genuina Maire. Fl. Afr. Nord. 2:18. (1953) (Based on P. bulbosa as misapplied by Maire to P. aquatica L.)

Phalaris bulbosa var. alata (Batt. and Trab.) Maire and Weiller in Maire. Fl. Afr. Nord. 2:18. (1953) (Based on P. tuberosa var. alata Batt. and Trab. P. bulbosa is misapplied by Maire to P. aquatica L.)

Phalaris bulbosa var. clausonis (Maire and Trabut) Maire and Weiller in Maire. Fl. Afr. Nord. 2:18. (1953) (Based on P. tuberosa var. clausonis Maire and Trabut. P. bulbosa is misapplied by Maire to P. aquatica L.)

Description

Perennial; culms from a dense crown or loose base with short rhizomes, culms often bulbous at the base, up to 1.5 m tall; panicle 1.5-11.0 cm long, 1.0-2.5 cm wide, usually cylindric, sometimes ovate-cylindric, occasionally lobed at the base; glumes 4.4-7.5 mm long, 1.0-2.0 mm wide, glabrous, rarely hirsute, broadly winged, the wing margin almost always entire, rarely somewhat erose; fertile floret 3.1-4.6 mm long, 1.2-1.5 mm wide, lanceolate, densely pubescent; sterile florets 1 or sometimes 2, 0.2-2.2 mm long, when 2 are present the lowermost is often less than 0.5 mm long; caryopsis 2.2-2.5 mm long, 1.2-1.3 mm wide, light brown, surface faintly striate; chromosome number $2n=28$, the chromosomes ca. 6-7 μ long at diakinesis.

Observations

One of the more interesting taxonomic problems within this species is that concerned with Phalaris tuberosa var. stenoptera (Hack.) Hitchc. (P. tuberosa=P. aquatica, see section on nomenclature), commonly called "Harding Grass" or "Toowoomba Canary Grass." Harding grass first appeared in Australia in the early 1880's. There are two accounts of its introduction into Australia: R. Harding (1884) published a short note in an obscure journal stating that seeds of this grass were received by him from the "Department of Agriculture, America." These seeds were subsequently planted in the nursery at Toowoomba, Australia under the name of P. commutata. The grown plants were later dug up and dumped in a corner where they continued to flourish. Harding later (about 1893) began to propagate and distribute the grass. Swart (1908) claims that a Mr. Charles Ross, manager of the state farm at Westbrook, Queensland, informed him that a Mr. Way, then curator of the Botanic Garden at Toowoomba (about 1888), received seed of P. aquatica from the Agricultural Department of New York, U.S.A. This seed was planted in the garden but much was lost due to extreme climatic conditions of that year. The only surviving material existed in out-of-the-way places such as hedgerows and rubbish heaps. Ross later began to propagate and distribute this material. Apparently there was a gap of several years between its relegation to waste areas and the systematic distribution for agronomic purposes.

Accepting either solution for its introduction into Australia, the facts are that it (1) was introduced into Australia and (2) that it grew at the Botanical Garden at Toowoomba for a period of years.

For some years the name P. commutata R. and S. was applied to this taxon. Ewart quotes Bertolini (place and date of Bertolini's publication not given) as saying that this name was based upon a composite specimen containing vegetative parts of P. aquatica and an inflorescence of P. minor. The original description would seem to refer to such a composite specimen as Bertolini discussed.

In 1908 Hackel described P. stenoptera based on plants and seeds sent to him by Ewart. This species, according to Hackel, was somewhat intermediate between P. arundinacea and P. aquatica.

In 1932 interest in Harding Grass was revived by Jenkin and Sethi of the Welsh Plant Breeding Station at Aberystwyth, Wales. These two investigators attempted crosses using P. arundinacea and P. aquatica as the female and male parents, respectively. The mostly sterile F_1 hybrids were intermediate between the two parents. Reciprocal crosses were not as successful. Back-crosses to either parent gave poor results although it was possible to obtain seedlings by using P. aquatica as the male parent. Further backcrossing to the P. aquatica parent yielded populations that were relatively fertile. Jenkins and Sethi, due partially to adverse experimental conditions, had little success in obtaining back-crosses using P. arundinacea as the male parent; however there was evidence that the pollen of this species did stimulate ovary development. Taxonomically one of the most interesting aspects of this cross was that the F_1 hybrids bore a strong similarity to Harding Grass which had so mysteriously appeared in Australia some thirty years previously. On the basis of this information, Jenkin and Sethi elaborated a hypothesis



Plate 5. Phalaris arundinacea, P. aquatica, and P. arundinacea x P. aquatica.

- a-d. Phalaris arundinacea; a. inflorescence, b. spikelets, c. florets, d. caryopsis.
- e-i. Phalaris aquatica; e. bulbous culm bases of var. aquatica, f. culm bases of Harding grass, g. spikelets, h. florets, i. caryopsis.
- j-l. Phalaris arundinacea x Phalaris aquatica; produced at Aberystwyth, Wales by T.J. Jenkins, drawings made from specimen in US collected by Jenkins (2lbs-1-2, July 13, 1928); j. spikelet, k. floret, l. culm bases.

for the hybrid origin of Harding Grass. They reasoned that since there was a period of time during which P. aquatica was growing more or less unobserved in the waste areas of the Toowoomba Botanic Garden, it could have crossed with P. arundinacea. Later, a series of back-crosses with P. aquatica developed the new hybrid which was called P. stenoptera by Hackel. The suggestion of hybrid origin was not new with Jenkin and Sethi. Ewart (1908) had mentioned the possibility but argued against it because Harding Grass had a high seed producing capacity. Jenkin and Sethi showed, however, that back-crosses to the P. aquatica parent and second, third, and even fourth generation plants from the F_1 hybrid had good seed producing capacity. Ewart did suggest that Harding Grass might be a hybrid between P. aquatica and the very different P. canariensis. The present author feels that the latter species is so different from Harding Grass that there must be virtually no possibility that a P. canariensis genome could have been involved in its origin. Kennedy (1917) also suggests a possible hybrid origin for Harding Grass.

Daveau (1926) described what he claimed to be a hybrid between P. nodosa (misapplied to P. aquatica by Daveau) and P. arundinacea. This supposed hybrid was named \times Phalaris monspeliensis by Daveau. The plant was found growing in the botanical garden at Montpellier, France and was collected by Loret.

Allan and Zotov (1930) considered the possibility of hybrid origin of Harding Grass but could find no information to support it.

Trumble (1935) obtained F_1 hybrids between P. aquatica and P. arundinacea but did not feel that the Australian plant represented the same taxon as P. tuberosa var. stenoptera.

In an effort to gather more information concerning the possible hybrid origin of this variety, the author examined herbarium specimens of all three taxa supposedly involved. Measurements were made of the inflorescence and spikelet parts. Special attention was paid to glume-wing size and shape, sterile floret number and size, and to the nature of the culm bases and underground plant parts. Of the features examined, the following seemed to possess considerable taxonomic importance: fertile floret length, glume length, sterile floret number and relative size, and the nature of the culm base and underground system. These characters are presented in graphic form in Figure 8. In this figure, each specimen is introduced by plotting its glume length against its fertile floret length. Shaded circles represent specimens of P. arundinacea having vigorous, long rhizomes and nonbulbous culm bases; half-shaded circles represent plants with rhizomes absent or very short, tufted growth habit, and nonbulbous culm bases; unshaded circles represent typical P. aquatica specimens with markedly bulbous culm bases. The number and relative length of the sterile florets is indicated by diagonal, upwardly-projecting lines. Two equal upward lines represent plants with two equal sterile florets; two unequal upward diagonal lines indicate specimens with one normal-length sterile floret (ca. 1.5 mm) and one very short sterile floret. The relative length of the lines indicates, roughly, the relative length of the sterile florets. A single diagonal line represents specimens having a single sterile floret; absence of projections indicates that both sterile florets were obsolete. Specimens used in the construction of this diagram were collected from all parts of the world.

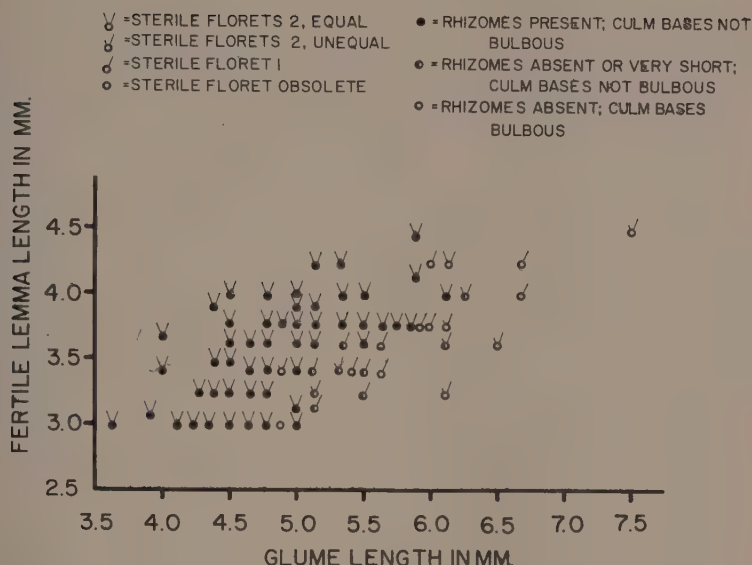


Figure 8. Relationship of growth habit and sterile floret type to fertile floret length and glume length in *Phalaris aquatica*.

From this diagram several population trends can be recognized. One trend, represented by shaded circles with equal projecting lines, has relatively short glumes and fertile florets, two equal sterile florets, well-developed rhizomes, and lacks bulbous culm bases. These are specimens of *P. arundinacea* and are typical of the species. Another trend, represented by unshaded circles and one projecting line, is composed of specimens having relatively long glumes and fertile florets, one sterile floret, bulbous culm bases, and lacks rhizomes. These are specimens of *P. aquatica* var. *aquatica* and are typical of the species from its native Mediterranean region. The specimens intermediate between these two trends are heterogeneous. Many different combinations of characters are represented in this group. Some of these plants have a tufted growth habit, one sterile floret or two unequal sterile florets, occasionally have very short rhizomes, and lack bulbous culm bases (these plants are represented by half-shaded circles with one projecting line or two, unequal, projecting lines). Others had bulbous culm bases and two unequal sterile florets (represented by unshaded circles with two, unequal, projecting lines). It is interesting to note that all of the specimens of the intermediate group were collected at botanical gardens or experimental farms. Only the specimens of *P. arundinacea* and those specimens of *P. aquatica* var. *aquatica* with a single sterile floret or no sterile florets were collected from native stands.

One of the more difficult aspects of the Jenkin and Sethi hypothesis is that there is, as they point out, no proof that P. arundinacea, one of the parents of this supposed Australian hybrid, was present at the critical time necessary for the cross to have taken place. The author has not seen any specimens from this area although Allen and Zotov (1930) report P. arundinacea from New Zealand. The absence of P. arundinacea from the herbaria does not necessarily negate the Jenkin and Sethi proposal. The plants supposedly involved in the production of this hybrid were cultivated in an experimental nursery; it is not uncommon to find that many of our most commonly cultivated plants are not represented in herbarium collections. Another aspect to consider is that perhaps the seed originally brought into Australia was of hybrid derivation. This latter idea seems quite attractive. The fact remains, however, that the artificial hybrids produced by Jenkin and Sethi do bear a very strong similarity to Harding Grass. By its very nature, the evidence presented for the hybrid origin of Harding Grass must remain somewhat circumstantial but the author feels that the hypothesis elaborated by Jenkin and Sethi provides the most suitable explanation for the origin of this entity.

Ruiz (1947) reduced P. aquatica (mistakenly called P. bulbosa by Ruiz) to a subspecies of P. arundinacea. The differences between P. aquatica and P. arundinacea are presented below:

1. P. aquatica has bulbous culm bases and a fibrous root system or is tufted, rarely with very short, poorly developed rhizomes; P. arundinacea has nonbulbous culm bases arising from strong rhizomes.

2. P. aquatica has glumes with well-developed, prominent wings; the glumes of P. arundinacea are commonly wingless. If winged, the wing is very narrow and inconspicuous.

3. The inflorescence of P. aquatica is usually not branched or lobed; the inflorescence of P. arundinacea is almost always branched or lobed.

4. The fertile floret of P. aquatica is broadly lanceolate, quite strongly flattened, and narrowly elliptic in cross-section; fertile florets of P. arundinacea are narrowly lanceolate and more or less circular in cross-section.

5. P. aquatica usually has one, occasionally two sterile florets. If two sterile florets are present they are markedly unequal. P. arundinacea always has two equal florets.

6. The caryopsis of P. aquatica is usually over 2 mm in length; the caryopsis of P. arundinacea is usually shorter than 2 mm.

In view of the numerous well-defined differences between the two species, the present author has maintained them as distinct.

Cytology and cytogenetics

Somatic chromosome numbers of $2n=28$ have been reported for this species by Trumble (1930), Jenkin and Sethi (1932), Parthasarathy (1939), Hanson and Hill (1935), Hutton (1953), and Ambathsa (1956). The chromosome count obtained by the present author is presented in Table 8.

Jenkin and Sethi (1932) studied cytologically the hybrid produced between P. arundinacea and P. aquatica. The P. arundinacea plant used in the production of the hybrid had a chromosome number of $2n=28$; P.

Table 8. Chromosome number from pollen mother cells of Phalaris aquatica L.

Collection	Seed source location	Chromosome number
Plant Introduction no. 202762 Anderson voucher no. 1209	Transvaal	2n=28

aquatica of the strain used in the experiment also had a chromosome number of $2n=28$. The chromosomes of P. aquatica were slightly larger than those of P. arundinacea. Both of the two parental species showed slight lagging of one or two bivalents. A chromosome number of $2n=28$ was also reported for the hybrid. The parental chromosomes could not be identified. At metaphase I in the F_1 hybrids twelve bivalents and four univalents were consistently formed. The univalents behaved erratically and were often lost. It is possible, but not proved, that the univalents in the F_1 correspond to the lagging bivalents occasionally occurring in both of the putative parents.

Ambathsa (1956) studied the hybrid between P. aquatica and P. minor that was reported by Trumble (1935). These hybrids were short-lived perennials. Laggards were observed at anaphase I and telophase I. Trivalents and quadrivalents were seen at metaphase I. The plants were highly sterile but produced good pollen. Partial synapsis showed that the two species may have some homologous chromosomes.

Nomenclature

Three incorrect names, P. bulbosa L., P. tuberosa L., and P. nodosa Murr., have been used for this species.

The first, P. bulbosa L., is a species of Phleum. A photograph (in GH) of the holotype in the Linnaean Herbarium, London, England, leaves no doubt that the holotype specimen is not in the genus Phalaris.

P. tuberosa L. has been widely used as the name of this species. This name, which was published in 1771, was antedated by Phalaris aquatica, published in 1855. Dr. C.E. Hubbard (personal communication) of the Royal Botanic Gardens, Kew, England, kindly supplied detailed descriptions of the holotypes of P. aquatica and P. tuberosa in the Linnaean Herbarium. These descriptions, in conjunction with the original descriptions by Linnaeus and photographs (in GH) of the specimens in the Linnaean Herbarium, serve to establish the identity of the names. The holotypes of these two names are both the same species. Thus Linnaeus gave different names to the same taxon. This is perhaps explained by the fact that one of the holotypes, that of P. tuberosa, is immature and in rather poor condition. Since P. aquatica was described sixteen years prior to P. tuberosa, the former name is the oldest available, legitimate name.

P. nodosa, as first described by Murray (1774), is presumably based upon P. tuberosa L. The description of P. nodosa provided by Murray is the same as that given by Linnaeus for P. tuberosa. In addition the phrase "Mant. 557," the place and page of publication of P. tuberosa,

was cited. P. tuberosa is the only Phalaris described on page 557 of the Mantissa.

Distribution

According to the older literature, Phalaris aquatica appears to have been native to the areas bordering the Mediterranean Sea. In recent years the forage possibilities of this species have been the subject of much agronomic investigation. This has resulted in wide distribution in grassland regions.

A map (Figure 9) gives the geographic origin of the specimens studied by the author.



Figure 9. Geographic distribution of Phalaris aquatica.

Selected specimens examined

ARGENTINA: Buenos Aires, cultivated, L.R. Parodi 5415 (US).

AUSTRALIA: New South Wales, R.A. Black 1183.007 (US); Queensland, Bunya Mts., M.S. Clemens 24-44 (US); Victoria, Canterbury (US); Western Australia, Warren River, W.M. Carne H.143 (US).

BRAZIL: Rio Grande do Sul, Pelotas, L. Esteves 25 (US).

CANADA: Quebec, Ottawa, Botanic Garden, D.C. McIntosh 1927 (US).

CHILE: Concepcion Prov., Reamuncho, E. Barros 7045 (US).

ECUADOR: Pichincha Prov., Uyumbicho, E. Asplund 7026 (US).

ENGLAND: Wales, Aberystwyth, cultivated, T.J. Jenkins (US).

FRANCE: Ajaccio, A. de Forestier (US).

GREECE: Corinth, Heldreich (US); Isle of Rhodes, Bastida, E. Bourgeau 155 (US).

ITALY: Girgenti, M. Gandoger (MO).

JORDAN: Amman, H.F. Mooney (MO).

MOROCCO: road between Marrakesh and Tanacourt, D. Fairchild, May 15, 1925 (US).

PORTUGAL: Coimbra, M. Ferreira 615 (US); Madeira Islands, M. Vahl, July 26, 1902 (US).

SYRIA: Aleppum, T. Kotschy, May 20, 1841 (MO).

TURKEY: Constantinople, W. Noewi 732 (MO).

UNION OF SOUTH AFRICA: Transvaal, Pretoria, cultivated, M. Pentz, Dec. 30, 1926 (US).

UNITED STATES: California, Humboldt Co., Loleta, J.T. Howell 13721 (US); District of Columbia, Washington, Grass garden, June 9, 1937 (US); Georgia, Experiment, P.I. no. 206710, seed source: Turkey (US); Hawaiian Islands, Maui, floor of Haleakala crater, O. Degener 10828 (US); Mississippi, Starkville, S.M. Tracy, May 25, 1891 (MO); Oregon, Corvallis, cultivated, H.A. Schoth, Jan. 4, 1934 (US); Texas, Renner Co., cultivated, D.S. Correll, June, 1958 (US); Virginia, Arlington Farms, cultivated, P.L. Ricker, July 6, 1923 (US).

URUGUAY: Montevideo Dept., sayugo, J. Schroder 79923 (US).

VENEZUELA: Merida, Otra Banda near Merida, T. Lasser 406 (US).

6. Phalaris truncata

Phalaris truncata Guss. Fl. Sic. Prod. Suppl. 18. (1832) (Holotype in NAP)

Phalaris aquatica Guss. non L. Fl. Sic. Prod. 1:69. (1827)

Phalaris truncata var. angustata Trab. in Batt. and Trab. Fl. Alg. Mon. 140. (1895)

Phalaris biattenuata Gand. Nov. Conspect. Fl. Eur. 486. (1910)

Phalaris brachystachys var. truncata (Guss.) Ruiz. Anal. Jard. Bot. Madrid. 8:492. (1947)

Phalaris truncata var. typica Maire and Weiller ex Maire. Fl. Afr. Nord. 2:20. (1953)

Phalaris truncata var. villiglumis Trabut ex Maire. Fl. Afr. Nord. 2:20. (1953)

Description

Perennial; culms to 200 cm tall; panicle 2.0-6.0 cm long, 0.8-1.6 mm wide, cylindric, occasionally ovoid-cylindric; glumes 5.5-6.3 mm long, 1.5-1.8 mm wide, glabrous or hirsute, truncate, winged, wing up to 1.0 mm wide; fertile floret 3.7-5.0 mm long, 1.2-1.4 mm wide, densely hairy, dark brown and shiny at maturity; sterile florets 2, 0.6-1.2 mm long, swollen and appearing somewhat fleshy, glabrous except for a tuft of hairs at the base; grain 2.8-3.0 mm long, 1.2-1.3 mm wide, subellipsoid, light brown; chromosome number $2n=12$, the chromosomes ca. 4-8 μ long at diakinesis.

Observations

The two swollen, somewhat fleshy sterile florets separate this species from all others of the genus except P. brachystachys. The differences between these species are enumerated and discussed under P. brachystachys.

Cytology and cytogenetics

Chromosome numbers of $2n=12$ have been previously reported for this species by Ambathsa (1956). The chromosome counts obtained by the author are reported in Table 9.

Table 9. Chromosome numbers from pollen mother cells of Phalaris truncata Guss.

Collection	Seed source location	Chromosome number
Plant Introduction no. 206712 Anderson voucher no. 1164	unknown	2n=12
Plant Introduction no. 240197 Anderson voucher no. 1173	Algeria	2n=12
Plant Introduction no. 240199 Anderson voucher no. 1163	Algeria	2n=12
Plant Introduction no. 240204 Anderson voucher No. 1189	Algeria	2n=12
Plant Introduction no. 240205 Anderson voucher no. 1188	Algeria	2n=12
Plant Introduction no. 240206 Anderson voucher No. 1176	Algeria	2n=12
Plant Introduction no. 240207 Anderson voucher no. 1172	Algeria	2n=12
Plant Introduction no. 240208 Anderson voucher no. 1183	Algeria	2n=12
Plant Introduction no. 240209 Anderson voucher no. 1177	Algeria	2n=12
Plant Introduction no. 240211 Anderson voucher no. 1195	Algeria	2n=12
Plant Introduction no. 240212 Anderson voucher No. 1181	Algeria	2n=12
Plant Introduction no. 240215 Anderson voucher No. 1182	Algeria	2n=12

Nomenclature

The type of Phalaris truncata Guss. (in NAP) was examined by the author. The drawings in Plate 6 were made from the type specimen.

Ruiz (1947) has reduced Phalaris truncata to varietal status under P. brachystachys Link. Reasons for maintaining these two as species are presented in the discussion of P. brachystachys.

Distribution

Phalaris truncata is restricted to the lands bordering the Mediterranean Sea. A map indicating the geographic origin of the specimens examined is presented in Figure 5.

Selected specimens examined

ALGERIA: Chir, vallée de l'Oued-Abdi, B. Balansa 717 (US); Constantine: C. Bolle, 1853 (MO); S. Choulette 289 (MO, US); Sidi Mecid, E.G. Paris 385 (MO); Kerrata, E. Reverchon 158 (F).

FRANCE: Herault, Perols, E. Mandon, June 18, 1893 (US).

ITALY: Sicily, Panormi, Todaro (US); Sicily, Sciafani, Todaro 1261 (US).

TUNISIA: Djirber, A. Letourneaux (US); Guiağyni, Colobria, 1824 (NAP) (Holotype).

7. Phalaris brachystachys

Phalaris brachystachys Link. Neu. Jour. Bot. Schrad. 1:134. (1806)

(Based on P. canariensis as described by Brotero in Fl. Lusit. 1:79. (1804)

Phalaris quadrivalvis Lag. Gen. et Sp. Nov. 3. (1816)

Phalaris nitida Presl. Cyp. et Gram. Sic. 26. (1820)

Phalaris vivipara Paoluc. Fl. Marchig. 19. (1891) pro syn.

Phalaris brachystachys var. robusta Thell. Fl. Adv. Montpel. 88 (1912)

Phalaris canariensis var. brachystachys (Link) Fedtsch. Bull. Jard.

Imp. Bot. Pierre le Grand. Suppt. 2. Part 1-a. 14:47. (1914)

Phalaris brachystachys var. typica Ruiz. Anal. Jard. Bot. Madrid. 8:492.

Description

Annual; culms to 90 cm tall; panicle ovoid, 1.5-4.0 cm long, 0.8-1.8 cm wide; glumes 6.3-8.5 mm long, 1.4-2.5 mm wide, with broad wing up to 1.0 mm wide, glabrous or hirsute; fertile floret 4.4-5.5 mm long, 1.3-1.8 mm wide, densely hairy, dark or brown and shiny at maturity; sterile florets 2, 0.6-1.2 mm long, swollen and appearing somewhat fleshy, glabrous except for a tuft of hairs at the base; grain 3.5-3.9 mm long, 1.5-1.7 mm wide, subellipsoid, light brown; chromosome number $2n=12$, the chromosome ca. 5-10 μ long at diakinesis.

Observations

Phalaris brachystachys and P. truncata form a closely-knit pair involving an annual and a perennial. The two are very close in overall morphology. There are, however, a number of relatively stable differences between the two populations, some of which are presented in tabular form in Table 10.

Table 10. Criteria used in separating Phalaris brachystachys Retz. and Phalaris truncata Gussone.

Character	<u>brachystachys</u>	<u>truncata</u>
duration	annual	perennial
shape of glume apex	abruptly pointed	truncate
inflorescence shape	ovoid to ellipsoid, occasionally cylindric	cylindric, occasionally ovoid to ellipsoid
glume length	6.3-8.5 mm	5.5-6.2 mm
fertile floret length	4.4-5.5 mm	3.7-5.0 mm
caryopsis length	3.5-3.9 mm	2.8-3.0 mm
caryopsis width	1.5-1.7 mm	1.2-1.3 mm

Ruiz (1947) reduced P. truncata to varietal status under P. brachystachys Link. In view of the data presented in Table 10, the author feels that these two species, though quite close morphologically, are nevertheless distinct enough to deserve nomenclatorial recognition.

Fedtschenko (1915) has reduced P. brachystachys to infraspecific status under P. canariensis. These two species differ radically in the nature of the sterile florets. P. canariensis has thin, somewhat papery, sterile florets that are more than half as long as the fertile floret (Plate 6, c); P. brachystachys has short rather fleshy, swollen sterile florets that are less than one-fourth as long as the fertile floret (Plate 6, f). In addition to this, the fertile florets of P. canariensis tend to be somewhat larger than those of P. brachystachys. The author feels that the differences between the two are too well marked and constant to be considered infraspecific rather than interspecific.

Cytology and cytogenetics

Chromosome numbers of $2n=12$ have been reported for this species by Miege (1939), Parthasarathy (1939), and Ambathsa (1956). The chromosome number obtained by the author is presented in Table 11.

Table 11. Chromosome number from pollen mother cells of Phalaris brachystachys Retz.

Collection	Seed source location	Chromosome number
Plant Introduction no. 202677 Anderson voucher no. 1186	unknown	$2n=12$

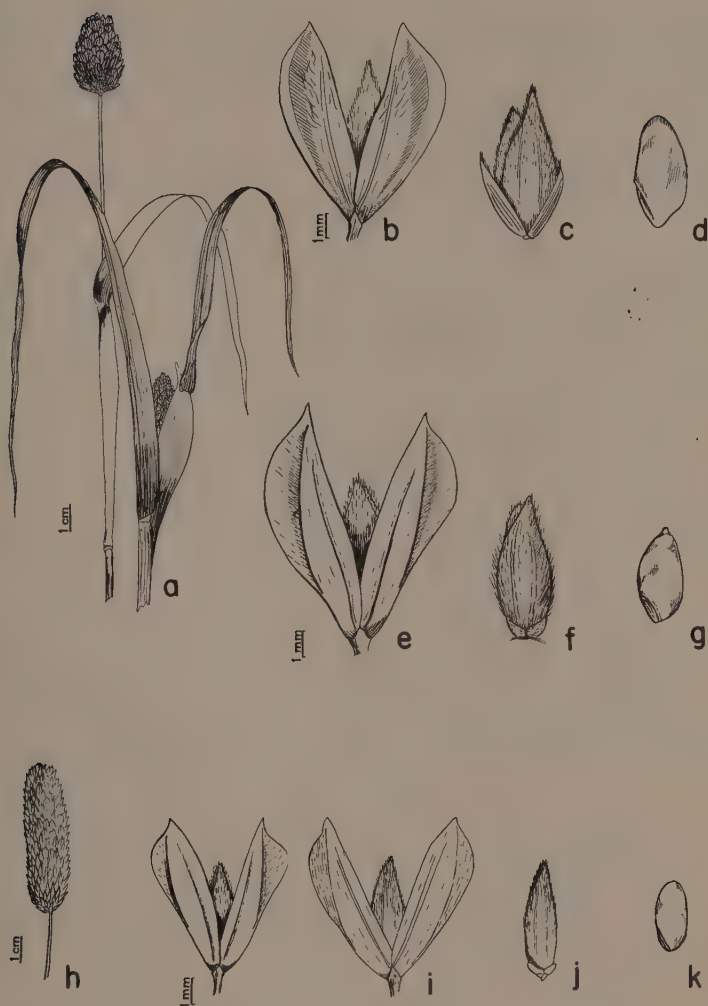


Plate 6. *Phalaris canariensis*, *P. brachystachys*, and *P. truncata*.

a-d. *Phalaris canariensis*; a. inflorescences, b. spikelet, c. floret, d. caryopsis.

e-g. *Phalaris brachystachys*; e. spikelet, f. floret, g. caryopsis.

h-k. *Phalaris truncata*; h. inflorescence, i. spikelets, j. floret, k. caryopsis.

There are three species in Phalaris having a basic chromosome number of $x=6$. They are: P. brachystachys, P. truncata, and P. canariensis. Parthasarathy (1939) suggests that the 12-chromosome species are derived from the 14-chromosome type by the fusion of two pairs of chromosomes with subterminal constrictions to give one pair with median constrictions. Further discussion of this will be found in the discussion of the cytology of the genus.

Parthasarathy (1939) reported several types of cytological abnormalities including inversion loops and lack of pairing. Meiosis in the author's material showed occasional irregular pairing.

Nomenclature

Phalaris brachystachys Link was described on the basis of a description of P. canariensis made by Brotero (1804). Brotero's original description leaves no doubt that he was referring to some species of Phalaris other than P. canariensis L. Brotero's description is of an annual plant with "valvulae accessoriae" (sterile florets) in the shape of small nectaries. P. brachystachys is the only member of the genus that is an annual and has sterile florets that are swollen and shaped like nectaries. Link (1806), in a review of Brotero's *Flora Lusitanica*, declared that P. canariensis, as described by Brotero, "ist neu" and provided the new specific epithet for the species. A later publication by Link (1826) included a more detailed discussion of the species and a complete description.

Distribution

P. brachystachys occurs primarily in the lands bordering the Mediterranean Sea and on the Canary Islands. It is an adventive at widely scattered locations in the United States. A map showing the geographic origin of the specimens studied is presented in Figure 10.



Figure 10. Geographic distribution of Phalaris brachystachys.

Selected specimens examined

CANARY ISLANDS: Gomera, San Sebastian, C.J. Pitard 388 (MO); Gran Canaria, Tafira, A.C. Cook 541 (F, MO, US); Teneriffe, La Questa, C.J. Pitard 700 (MO).

CYPRUS: Kanli, A. T. Semple 294 (US); Paphos, M. Haradjian 728 (MO, US).

FRANCE: Beziers, Theveneau, June 1, 1869 (MO); Montpellier, J. E. Planchon (US); Paris, Jeanpert, May 30, 1911 (F); Port Juvenal, naturalized, Touchy 1039 (F); Toulon, St. Marguerite, A. Theveneau, May, 1865 (US).

IRAQ: Daltawah, barley fields, E. R. Guest 1409 (US); Jebel Golat between Ain Tellawi and Balad Sinjar, H. Field and Y. Lazar 441 (F, US).

ITALY: Bologna, F. Cavara (US); Bologna, A. Fiori (US); Firenze, M. F. Spencer, May 21, 1893 (F); Sicily, Palermo, Todaro (US); Tuscany, Pisa, Savi 2161 (F).

JORDAN: Hebron, T. Kotschy 437 (US); Jerusalem, F. J. Meyers 686 (F).

LEBANON: Beirut, Jeanpert (F); Beirut, Post (US).

MADEIRA ISLANDS: Kuy 2682 (US).

MOROCCO: Dj Habibi, M. Gandoger, 1910-11 (MO); R'bat, M. Gandoger 1910-11 (MO).

PORTUGAL: Coimbra, A. Kneucker 616 (US); Estremadura, Campo-lide, A. R. da Cunha, May, 1890 (US).

SWEDEN: Malmo, Lundgren, 1864 (F).

SWITZERLAND: Champs Honneur, C. Thiebaut, April 30, 1877 (F).

UNITED STATES: California, Butte Co., Nelson, A. A. Heller 5446 (F, MO, US); Missouri, Laclede Co., Horseshoe Pond, G. Moore, June 30, 1938 (F); Oregon, Linnton, near Portland, W. N. Suksdorf 1904 (US).

8. Phalaris canariensis

Phalaris canariensis L. Sp. Pl. ed. 1. 54 (1753) (Holotype in LINN; photograph of holotype in GH)

Phalaris ovata Moench. Meth. Pl. 208. (1794)

Phalaris avicularia Salisb. Prodr. Stirp. 17. (1796)

Phalaris canariensis var. nigra Stokes. Bot. Mat. Med. 1:135. (1812)

Phalaris canariensis var. subcylindrica Thell. Viert. Naturf. Ges. Zurich. 56:271. (1912)

Phalaris canariensis f. vivipara Junge. Jahrb. Hamb. Wiss. Anst. 30:123. (1913)

Phalaris canariensis var. bracteata Jans. and Wacht. Nederl. Kruidk. Archief. 6:142. (1916)

Phalaris canariensis var. tenuis Jans. and Wacht. Nederl. Kruidk. Archief. 52:213. (1942)

Phalaris canariensis var. villosula Jans. and Wacht. Nederl. Kruidk. Archief. 52:213. (1942)

Phalaris canariensis f. colorata Jans. and Wacht. Nederl. Kruidk. Archief. 52:213. (1942)

Description

Annual; culms erect, 30-100 cm tall; panicle ovate to oblong-ovate, 1.5-4.0 cm long, 1.5-2.0 cm wide, spikelets broad, imbricate; glumes

7.0-10.0 mm long, pale green with darker green longitudinal stripes, keel winged, broadened upward, strigose or glabrous on wingless portion; fertile floret acute, 4.8-6.8 mm long, densely appressed-pubescent; sterile florets 2, 2.5-4.5 mm long, broad and somewhat chaffy, sparsely pubescent; grain 3.9-4.2 mm long, 1.4-1.7 mm wide, light brown, surface faintly striate; somatic chromosome number $2n=12$, the chromosomes ca. 5-9 μ long at diakinesis.

Observations

P. canariensis, commonly called Canary Grass, is readily separable from all other species in the genus by its relatively large, foliaceous sterile florets which are always more than 2.5 mm in length and at least 1.5 mm wide (Plate 6, c). Phalaris brachystachys is grossly similar but always has smaller, swollen, sterile florets which are never longer than 1.2 mm (Plate 6, f). No intermediates are found between these species.

P. canariensis is used widely in seed mixtures for pet birds. Selschop and Wolfaardt (1952) discussed the commercial production of bird seed in South Africa. According to these authors, the best yields are obtained when seed is grown under irrigation or with about twelve inches of rainfall in the five-month period required for it to mature. Warm, low-altitude areas seem to provide the best environmental conditions. From 30 to 60 pounds of Canary Grass seed per morgen (about 2.1 acres) are sown in May. In frost-free areas planting may be as late as September. Yields are reported to run from 1200 to a maximum of 2000 pounds per morgen.

Cytology and cytogenetics

Chromosome numbers of $2n=12$ have been reported by Church (1929), Avdulov (1931), Katterman (1931), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), and Ambathsa (1956). Nakajima (1933) reports a chromosome count of $2n=28$. The count obtained by the present author is presented in Table 12.

Table 12. Chromosome count from pollen mother cells of Phalaris canariensis L.

Collection	Seed source location	Chromosome number
Plant Introduction no. 174299 Anderson voucher no. 1233	Turkey	$2n=12$

Church (1929) and Parthasarathy (1939) both report meiosis to be normal in this species. Meiosis in the author's material likewise appears to be normal.

The chromosome count of $2n=28$ reported by Nakajima (1933) is certainly quite different from the other counts reported. A voucher specimen was not cited and there can be no sure way to identify the specimen from which the count was made. On the basis of all of the counts made by other workers it would seem possible that Nakajima had come species other

than P. canariensis. The illustration included with Nakajima's report shows 14 pairs of relatively small chromosomes. Meiotic chromosomes in the author's material were quite large; certainly they appeared much larger than those illustrated by Nakajima. Until positive identification of the original material used by Nakajima is presented this report must remain open to some question.

Ostergren (1957) has experimentally produced autotetraploids ($2n=24$) and aneuploids ($2n=21, 23$), in P. canariensis by a pressurized nitrous oxide technique. No information on the morphology was included.

Nomenclature

Phalaris canariensis is one of two species of Phalaris described by Linnaeus in 1753 that can be correctly placed in this genus. Since Linnaeus did not specifically refer to any particular specimen in his herbarium as a basis for his description, it is necessary to choose a lectotype for the species. Accordingly sheet number 78.1 of the Linnean herbarium (LINN) is hereby designated as the lectotype of P. canariensis. Dr. C.E. Hubbard of the Royal Botanic Gardens, Kew, England (personal communication) kindly furnished a detailed description of the specimens on this sheet. This description leaves no doubt as to the species involved.

Distribution

Raius (1694) gave Sicily, Italy, and southern France as the range of Canary Grass. Unfortunately it is not possible to be sure that Raius was referring to P. canariensis alone or whether he was including several of the species in Phalaris that were probably native to the area. Linnaeus (1753) listed the habitat of this species as southern Europe and the Canary Islands. Early floras agree substantially with this distribution. The widespread interest in this species as a source of bird seed, coupled with its over-all viability, probably aided it in becoming adventive in many areas not included in its original range. Adventive individuals are frequently found growing in refuse dumps and ballast deposits.

A map (Figure 11) presents the geographic origin of the specimens examined by the author.

Selected specimens examined

ARGENTINA: Buenos Aires, between Buenos Aires and La Plata on railroad, W.J. Eyerdam, A.A. Beetle 23154 (MO); Tucuman Prov., Rio Sali, S. Venturi 4560 (US).

AUSTRIA: Salzburg, Dreifuss, August 29, 1872 (MO).

BELGIUM: Brussels, Tilvorde, J.D. Vits, June 30, 1930 (US).

BERMUDA: Paget, cultivated ground, S. Brown, N.L. Britton, P. Bisset (US).

BOLIVIA: La Paz, O. Buchtien 239 (US).

BRAZIL: Minas Geraes, Pocos de Caldas, A. Chase 10680 (US).

CANADA: Alberta, Edburg, A.H. Brinkman, Aug. 3, 1927 (US); British Columbia, Yoho Park, Naturalized at field elevation of 4060 feet, T. Ulke GI (F); Manitoba, Ashland, T. Morong (F); Nova Scotia, Kempt Shore, E. Mosher, Aug. 31, 1918 (US); Ontario, Kingston, J. Fowler, June 14, 1898 (US); Saskatchewan, Regina, J. Lunell, Sept. 9, 1902 (US).

CHILE: Valparaiso, Bro. Claude-Joseph 3514 (US).



Figure 11. Geographic distribution of Phalaris canariensis.

CHINA: Fukien Prov., Foochow, Metcalf 953 (US).

CUBA: Havana, Bros. Leon and Eckman 4265 (US).

DENMARK: Copenhagen, H. Mortensen, Aug. 24, 1889 (MO).

ENGLAND: Hove, Brighton, C.B. Clarke CC102 (US); St. Phillip's Marsh, C. Somers 1490 (MO).

FRANCE: Antibes, Thuret, June 4, 1861 (F); Paris, Gentilly, Jeanpert, July 15, 1918 (F); Montpellier, Cintract, May 27, 1888 (US).

GERMANY: Karlsruhe, A. Kneucker, July, 1900 (MO); Schmiedeberg, G. Hieronymus, Aug. 18, 1884 (US).

HONG KONG: Aberdeen, Y.W. Taem 1403 (US).

HUNGARY: Mestlalajon, A. de Degen 259 (US).

ITALY: Firenze, M.F. Spencer, May 21, 1893 (F); Corsica, Ilerousse, P. Aellen 342 (MO).

MEXICO: Puebla, vic. Puebla, base del Cerro Guadalupe, G. Arsene, Sept. 1, 1907 (US); Rosario, J.N. Rose, July 26-29, 1897 (US).

NETHERLANDS: Rotterdam, G. Ver Meulen, Aug. 24, 1927 (US).

NORWAY: Vestre Aker, O. Andersen, July 8, 1907 (US).

PERU: Lima, R.J. Seibert 2323 (MO, US); Puno, Salcedo, Saukup, Feb., 1938 (F).

SPAIN: Lisiere des champs a Fiscal, Aragon, terrain-calcaire, G. Gautier, June 14, 1879 (F); Porto Santa Maria, E. Bourgeau 505 (US).

SWEDEN: Malmo, B. Lundgren, 1864 (F).

SWITZERLAND: Winterthur, Hirzel (MO); Zurich, Molasse, F.G. Stebler and C. Schroter 9 (US).

UNION OF SOUTH AFRICA: Pietermaritzburg, A.P. Gooseus 154 (US).

UNITED STATES: Alaska, Fairbanks, A.S. Hitchcock 4577 (US); Arkansas, Little Rock, G. Letterman (MO); California, Yreka, G.D. Butler 488 (US); Colorado, Denver, E.L. Hughes 22 (GH); Connecticut, Bridgeport, E.H. Eames, July 31, 1895 (GH, US); Delaware, Wilmington, A. Commons, July 8, 1897 (US); District of Columbia, Washington, T.H. Kearney, June 4, 1898 (US); Illinois, Wheaton, W.S. Moffatt 814 (MO);

Indiana, Noble Co., east of Ligonier, C.C. Deam 14317 (US); Iowa, Des Moines, C.R. Ball 29 (US); Kansas, Topeka, E.A. Popenoe, June 15, 1879 (US); Maine, Camden, G.G. Kennedy, July 21, 1902 (GH); Maryland, Berlin, F.L.J. Boettcher, June 13, 1898 (F); Massachusetts, Dorchester, "dump," Churchill Estate, J.R. Churchill, Sept. 19, 1911 (GH, MO); Michigan, Cheboygan Co., Cheboygan city dump, L.H. Harvey 671 (US); Minnesota, Springfield, E.P. Sheldon, July, 1891 (GH); Missouri, East St. Louis, H. Eggert, July 4, 1887 (MO); Montana, Bozeman, J.W. Blankinship, Sept. 26, 1898 (NDA); Nebraska, Kearney, C.L. Shear 269 (MO, US); New Jersey, Weehawken, W.M. van Sickle, July 10, 1895 (US); New York, New York City, 86th Street, W.H. Reggett, June 15, 1866 (GH); North Dakota, Devil's Lake, T.T. Anderson, August 10, 1905 (NDA); Ohio, Portage Co., Garrettsville, R.J. Webb 1411 (GH); Oregon, Portland, W.N. Suksdorf 2758 (US); Pennsylvania, Lancaster Co., Columbia, A.P. Garber 1869 (US); Rhode Island, Providence, common on waste ground, J.F. Collins, July 9, 1892 (GH); South Carolina, Columbia, K.A. Taylor, May, 1890 (F); South Dakota, Brookings, J.J. Thornber, Aug. 25, 1893 (MO); Texas, Gillespie Co., G. Jermy 36 (MO); Virginia, Smyth Co., Marion, J.K. Small, July 8, 1892 (F, GH, US); Washington, Point Haddock, N.L. Gardner 33 (US); West Virginia, Wheeling, H.N. Mertz, July 1877 (US); Wisconsin, Sturgeon Bay, J.K. Schuette, July 4, 1900 (F); Wyoming, Mammoth Hot Springs, E.A. Kearns 3376 (US).

URUGUAY: Montevideo, Atahualpa, Herter 558 81444 (US).

9. Phalaris angusta

Phalaris angusta Nees ex Trin. Sp. Gram. Icon. Descr. vol.1. pl.78. (1828)

Phalaris chilensis Presl. Rel. Haenk. 1:245. (1830) (Holotype in PR)

Phalaris ludowiciana Torr. ex Trin. Mem. Acad. Sci. St.-Petersb.

Ser.6. 5:56. (1840) pro syn.

Phalaris laxa Spreng. ex Steud. Nom. Bot. ed.2. 2:315. (1841) pro syn.

Phalaris intermedia var. angusta (Nees) Chap. Fl. So. U.S. 569 (1860)

Phalaris intermedia var. angustata Beal. non Schlecht. Grasses in N.A. 2:182. (1896) (Photograph of type in US)

Phalaris angusta f. macra Hack. ex Stuckert. Anal. Mus. Nac.

Buenos Aires. Ser.3. 14:63. (1911) (Clastotype in US)

Phalaris angusta var. bracteata Jans. and Wacht. Nederl. Kruidk. Archief. 6:139. (1916)

Phalaris angusta var. robusta Jans. and Wacht. Nederl. Kruidk. Archief. 6:139. (1916)

Phalaris angusta f. composita Jans. and Wacht. Nederl. Kruidk. Archief. 6:139. (1916)

Phalaris angusta f. interrupta Jans. and Wacht. Nederl. Kruidk. Archief. 6:139. (1916)

Description

Annual; culms to 150 cm tall; panicle narrow and cylindric, 2.5-17.0 cm long, 0.6-1.5 cm wide; spikelets usually densely imbricate, lying almost parallel with the inflorescence axis; glumes 2.9-5.5 mm long, 0.6-1.1 cm wide, apex usually naviculate, occasionally acute, nerves scabrous along most of the length, internerve areas scabrous near the

base of the glume; fertile floret 2.2-3.8 mm long, 0.9-1.5 mm wide, densely pubescent and shiny; sterile florets 2, 0.7-1.5 mm long, a tuft of hairs at the base; grain 1.4-1.6 mm long, 0.7-0.9 mm wide, somewhat flattened; chromosome number $2n=14$, the chromosomes ca. 4-7 μ long at diakinesis.

Observations

Phalaris angusta, P. amethystina, P. caroliniana, P. platensis, and P. lemmonii are members of a species complex indigenous to several areas in the Americas. P. platensis and P. lemmonii differ from the remaining three in that they have plump, turgid fertile florets which are almost round in cross section. The fertile florets in these two species are densely pubescent with spreading hairs except for the naked, sharply acuminate apex. P. angusta, P. amethystina, and P. caroliniana have somewhat flattened fertile florets that are more or less evenly pubescent, including the acute, tapering apex. A comparison of P. angusta, P. caroliniana, and P. amethystina for several characters is presented in Table 13.

Table 13. Comparison of Phalaris angusta, P. caroliniana, and P. amethystina.

Character	<u>P. angusta</u>	<u>P. caroliniana</u>	<u>P. amethystina</u>
glume length	extreme 2.9 mm mean 3.7 extreme 5.5	4.2 mm 5.4 6.7	4.7 mm 5.3 6.2
shape of glume apex	usually naviculate, occasionally acute	acute	acute
glume lateral nerve pubescence	scabrous	glabrous, very rarely slightly scabrous	scabrous
fertile floret length	extreme 2.1 mm mean 2.8 extreme 3.8	3.0 mm 3.4 4.7	3.3 mm 3.6 4.2
sterile floret length	extreme 0.7 mm mean 1.2 extreme 1.5	1.5 mm 1.9 2.5	1.5 mm 1.7 1.9
caryopsis length	1.4-1.6 mm	2.0-2.3 mm	2.1-2.2 mm
inflorescence length	extreme 2.5 cm mean 7.7 extreme 17.0	1.0 cm 3.8 7.0	2.7 cm 3.7 4.5



Plate 7. Phalaris angusta, P. californica and P. maderensis.

- a-d. Phalaris angusta; a. inflorescence, b. spikelets,
c. florets, d. caryopsis.
- e-h. Phalaris californica; e. inflorescence, f. spikelet,
g. floret, h. caryopsis.
- i-k. Phalaris maderensis; i. inflorescence, j. spikelets,
k. floret.

As can be seen from Table 13, the average lengths of the glumes, fertile florets, sterile florets and inflorescences are somewhat different from those of P. caroliniana and P. amethystina. The most pronounced quantitative difference seems to be that of the sterile floret length. Sterile florets of P. angusta are shorter than 1.5 mm long; those of the other two species are 1.5 mm long or longer. The inflorescence of P. angusta is rather long and narrow as compared to P. caroliniana and P. amethystina. Qualitatively, the shape of the glume apex seems to be a good differentiating feature. Glume apices of P. angusta are usually naviculate (Plate 7, b), occasionally acute; glume apices of P. amethystina (Plate 8, f) and P. caroliniana (Plate 9, f) are almost always acute.

Some specimens of P. angusta collected in California differ from the typical form in several features. The inflorescences and spikelets are larger. The glume apices are quite acute, certainly not as naviculate as those of collections of P. angusta made in the southeastern United States; the lateral nerves are not as densely scabrous as those of specimens from the remainder of the range; the inflorescences are not as densely imbricate, the spikelets tend to diverge from the inflorescence axis at about a forty-five degree angle. Morphologically, these specimens resemble collections of P. caroliniana; the most prominent differences are the scabrous lateral glume nerves, a feature not found in typical P. caroliniana collections, and the much larger, somewhat lobed inflorescences, likewise not characteristic of P. caroliniana. Overlap of the ranges of P. angusta and P. caroliniana occurs both in the southeastern United States and in California. On the basis of the very limited number of specimens of this large P. angusta seen by the author, it does not seem wise to more than suggest that possible introgression has occurred or is occurring between these two taxa. Further work, especially attempts at crosses and extensive field studies, is needed to determine the nature of the relationships within this species complex.

P. angusta f. macra Hack. ex Stuck. is based upon a depauperate specimen collected in Argentina. A fragment of the type is in US. This form differs from typical P. angusta only in being very short (less than 20 cm) and having very small inflorescences. Morphologically, the spikelets do not differ noticeably from those of the typical form.

The numerous named varieties of Jansen and Wachter (1916) are apparently extremes of the total variation pattern with respect to inflorescence shape and size.

Cytology and cytogenetics

Saura (1943) and Ambathsa (1956) report a chromosome number of $2n=14$ for P. angusta. The present author's chromosome count for this species is presented in Table 14.

Meiosis in the material studied by the author appeared normal.

Nomenclature

The first description of this species is that of Trinius in 1828. This description was credited to Nees ab Esenback but no place of publication by Nees was given by Trinius. The well-drawn plate accompanying Trinius' description leaves no doubt as to the typification of the species. Nees himself provided a full description in 1829.

Table 14. Chromosome number from pollen mother cells of Phalaris angusta Nees ex Trin.

Collection	Seed source: location	Chromosome number
Plant Introduction no. 202391 Anderson voucher no. 1184	Argentina	2n=14

Distribution

Most of the specimens examined by the author were collected in prairie and grassland areas in the southern United States and South America. Occasional adventives have been collected in the Union of South Africa. A map (Figure 12) gives the geographic origin of the specimens seen by the author.

Figure 12. Geographic distribution of Phalaris angusta.

Selected specimens examined

ARGENTINA: Buenos Aires Prov.: Boradero, Rio Pintas, A. Burkart 8508 (F, US); Delta of Rio Parana, W.J. Eyerdam and A.A. Beetle 23050 (MO); Chaco Prov., Las Palmas, P. Jorgensen (MO, US); Entre Rios Prov., Parana, Isla Puentes, I. Morel 10089 (US); Isla de Frances, Fiente a Rosario, A. Burkart 8807 (F); Rio Negro Prov., General Roca, W. Fischer 268 (F, MO, US); Tucuman Prov., Tafi, El Siambon, Schreiter 6876 (F, US).

BOLIVIA: Pucara, Valle Grande, St. Cruz, among wheat, S. Spiaggi 56 (US).

BRAZIL: Montenegro, Fazenda Paguete, P.N. Capparelli 552 (US); Rio Grande do Sul: Barro do Dibeiro, p. Guaiba, B. Rambo 37987 (US); Porto Alegre, C.A.M. Lindman A623 (US); Porto Alegre, Vila Manresa, B. Rambo 544533 (US); Pareci, Municipio Montenegro, B. Rambo 26647 (US).

CHILE: Yerba Buena, S. Venturi 986 (US).

ECUADOR: Azuay Prov., 3-8 km north of Sevilla de Oro, W.H. Camp E-5217 (MO).

UNION OF SOUTH AFRICA: Cape Peninsula, Bishopscourt, T.M. Salter 9054 (MO); Middleburg, cauliflower field, W. Long 8223 (MO, US).

UNITED STATES: California: Alameda Co., Alameda, Bolander, July 4, 1866 (MO); Los Angeles Co., Los Angeles, G.B. Grant 970 (F); Mendocino Co., Ukiah, Bolander 38 (US); San Bernardino Co., hills west of Colton, S.B. Parish 2165 (US); San Diego Co., Brooks, C.G. Pringle, May 1, 1882 (F, US) (Isotype, P. intermedia var. angustata Beal); San Luis Obispo Co., Los Osos valley, R.F. Hoover 7182 (US); Santa Cruz Co., Santa Cruz, C.L. Anderson, 1888 (US); Solano Co., 15 miles northwest of Rio Vista, I. Wiggins 5863 (F); Tulare Co., near Visalia, F.V. Coville and F. Funston 1282 (US); Georgia, Savannah, D.E. Eyles 6943 (GH); Louisiana: New Orleans, City Park, W.M. Canby, April 2, 1900 (US); Pointe a la Hache, A.R. Langlois, May 6, 1885 (US); Mississippi, Stoneville, P.R. Henson, May, 1932 (US); Oregon, Curry Co., 5 miles north of mouth of Euchre Creek, M.E. Peck 14653 (US); Texas: Galveston, F. Lindheimer, April, 1843 (MO); Sabine Pass, J. Reverchon, April 24, 1903 (MO).

URUGUAY: Canelones Dept., Aguas Corrientes, W.G. Herter 98074 (F); Canelones Dept., Montevideo, J. Arechavaleta 52 (US); Florida Dept. Arroyo Mansavillagra, Gallinal 5824 (US); La Palma, W.G. Herter 1037c (MO, US); Rio Negro Dept., Cerro Largo, Palleros, Rosengurt B-213 (US); San Jose Dept., Santa Lucia, C. Osten 21698 (US).

10. Phalaris californica

Phalaris californica Hook. and Arn. Bot. Beechey Voy. 1:161. (1838)
(Clastotype in US)

Description

Perennial; culms erect, up to 150 cm tall; panicle ovoid to oblong, 1.5-5.0 cm long, 1.0-3.0 cm wide, more or less truncate at the base; spikelets loosely imbricate; glumes 5.0-8.0 mm long, 0.9-1.6 mm wide, acute to somewhat acuminate, without wing or very narrowly winged at the apex, mid-nerve slightly scabrous, glume tips often tinged with

purple at maturity; fertile floret 3.5-5.0 mm long, 1.0-1.5 mm wide, sparsely pubescent; sterile florets 2, 1.8-3.3 mm long, densely pubescent; grain 2.4-2.6 mm long, 0.9-1.1 mm wide, cylindric, red-brown at maturity; chromosome number, $2n=28$, the chromosomes ca. 4-7 μ long (Ambathsa, 1956).

Observations

P. californica is a tufted perennial with the culms arising from a dense underground crown. The best distinguishing features are the short, relatively broad inflorescence (Plate 7, e), wingless (or very narrowly winged), often purple-tinged glumes (Plate 7, f), and the perennial habit. P. arundinacea is the only other perennial with wingless glumes. P. arundinacea spreads by means of extensive underground rhizomes; P. californica has no rhizomes. In addition, the caryopsis of P. arundinacea is relatively small, being 1.5-2.0 mm long (Plate 5, d); the caryopsis of P. californica is 2.4-2.6 mm long (Plate 7, h). The inflorescence of P. arundinacea is usually long and more or less narrowly cylindrical with a tapering or lobed base (Plate 5, a); that of P. californica is broadly cylindrical with a truncate base (Plate 7, e). All of the other perennial species in this genus have broadly winged glumes.

Cytology and cytogenetics

Stebbins and Love (1941) and Ambathsa (1956) report a chromosome count of $2n=28$ for this species. No material was available to the present author for study.

Nomenclature

A portion of the holotype of P. californica is in the United States National Museum and was examined by the author. This type represents the species as commonly understood today.

Distribution

P. californica is restricted to California and Oregon. Hitchcock (1950) reports that this species grows in ravines and open moist ground. A map (Figure 13) gives the geographic origin of the specimens examined during the course of this study.

Selected specimens examined

UNITED STATES: California: Contra Costa Co., Pt. Isabel, J. Burt Davy, April, 1897 (US); Del Norte Co., Douglas Park, J. W. Thompson 4509 (MO); Marin Co., San Rafael, J. W. Blankinship 58 (GH, US); Mendocino Co., Mendocino, J. McMurphy 456 (US); Monterey Co.: King City, J. Swallen 617 (US); Lime-kiln Creek, J. B. Davy 7706 (US); Moss Beach, Pacific Grove, A. Chase 5660 (US); Sta. Lucia Mts., A. Eastwood, May 1-12, 1897 (US); San Luis Obispo Co., Nipoma, W. H. Brewer 418 (US); San Mateo Co.: Crystal Springs Lake, A. D. E. Elmer 4699 (MO, US); Lake Pelaracitos, J. B. Davy 725 (US); Santa Clara Co.: Congress Springs, A. S. Hitchcock, June 22, 1908 (US); foot hills west of Los Gatos, A. A. Heller 8568 (GH, ISC, MO, US); Sonoma Co., Sherwood, A. S. Hitchcock, June 26, 1908 (US); Angel Island, H. N. Bolander 1529 (F, GH, US); Mendocino coast, H. H. Bolander 6123 (F, MO, US); Oregon, Curry Co., Chetco River, by the sea, T. Howell, June 11, 1884 (F, GH, US).

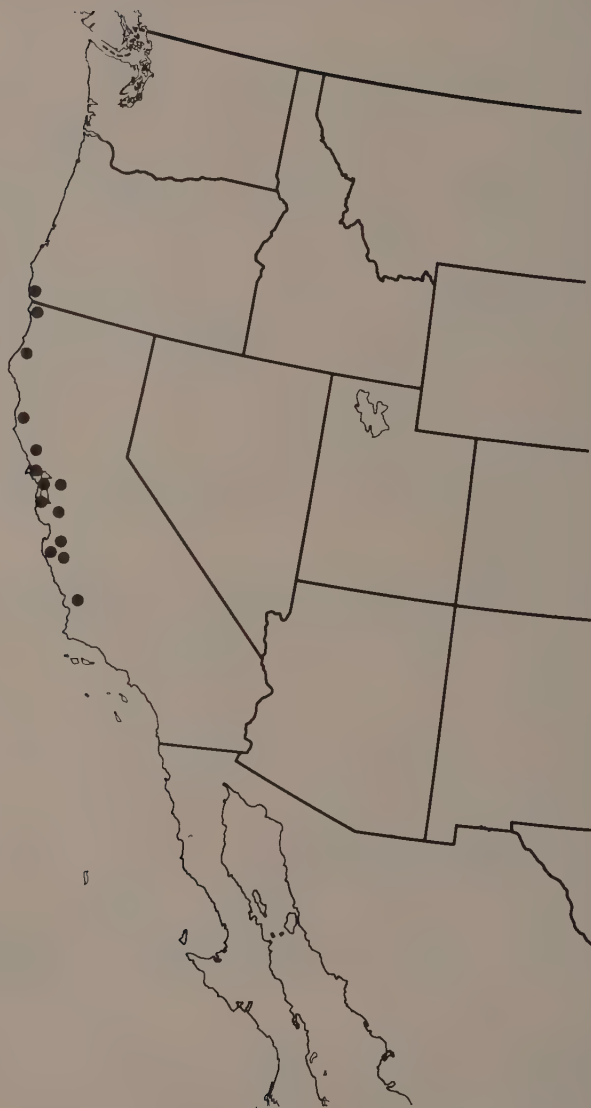


Figure 13. Geographic distribution
of Phalaris californica.

11. Phalaris maderensis

Phalaris maderensis (Menezes) Menezes. As Gramineas do archipelago da Madera. 23. (1906)

Phalaris coerulescens var. maderensis Menezes. Cat. Phanerogam. Madera Porto Santo. 57. (1894)

Description

Annual; roots fibrous; culms 10-50 cm tall, caespitose; panicle 2.5-5.0 cm long, ovate-oblong to cylindric; glumes 4.5-4.8 mm long, 1.4-1.5 mm wide, truncate, winged at the tip, glabrous, pale or sometimes tinged with purple; fertile floret 3.2-3.4 mm long, 1.2-1.3 mm wide, densely pubescent; sterile floret 1, 1.3-1.4 mm long, slightly pubescent along outer edge; grain about 1.8 mm long, 0.7 mm wide, pale brown with surface somewhat striate; chromosome number unknown.

Observations

Only one specimen referable to P. maderensis was available for study. On the basis of this limited material it seems to be a well-defined species. Only two other species in the genus have only one sterile floret. These are P. aquatica and P. minor. The former is a perennial, often with bulbous culm bases and has much larger spikelets. In addition, the glumes of P. aquatica are not truncate but are quite acute (Plate 5, g). P. maderensis is an annual and has small, more or less truncate spikelets in comparison to P. aquatica. The differences between P. minor and P. maderensis are a little more elusive. P. minor has pointed glumes that usually have the margin of the glume wings erose-denticulate (Plate 4, a). The glumes of P. maderensis are more or less truncate and have the margins almost entire (Plate 7, j). The single specimen available for study had a narrowly cylindrical inflorescence (Plate 7, i) about 4 cm long; inflorescences of P. minor are often ovate-oblong; when cylindric they are much wider than that of the specimen of P. maderensis.

The description of P. maderensis presented in this paper is drawn partly from Menezes' original description and partly from the specimen seen by the author.

Cytology and cytogenetics

No material of P. maderensis was available for cytological study. Chromosome numbers in this species are unknown.

Nomenclature

Menezes first named this taxon as a variety of P. coerulescens (1894). Twelve years later he elevated it to specific rank (1906). The type specimen of this species was not seen, however, Menezes' very complete description leaves no doubt as to the taxon referred to.

Distribution

The only location from which the author has seen collected material is on the island of Porto Santo off the northwest coast of Africa. Menezes gives Porto Santo as the place of collection of the type specimen.

Specimen examined

PORTO SANTO ISLAND: Kuy, Ilheu dos Embarcaderos. (US 1715395).

12. Phalaris amethystina

Phalaris amethystina Trin. Mem. Acad. Imp. Sci. St. Petersburg.

Ser. VI, 2de part. 5:56. (1840)

Phalaris berteroniana Steud. Syn. Pl. Glum. I. Gramineae. 11. (1855)

Phalaris robinsoniana Steud. Syn. Pl. Glum. I. Gramineae. 11. (1855)

Phalaris colchaguensis Phil. Linnaea. 33:276. (1864)

Description

Annual; culms to 60 cm tall, glabrous; panicle 1.5-4.5 cm long, 1.0-1.4 cm wide, ovate-cylindric; spikelets rather loosely imbricate, diverging from the panicle axis; glumes 4.7-6.2 mm long, 0.8-1.1 mm wide, somewhat winged, the wings sometimes obscure, acute to acuminate, glume lateral nerves scabrous on lower one-half; fertile floret 3.2-4.2 mm long, 1.0-1.6 mm wide, densely pubescent, somewhat flattened; sterile florets 2, 1.5-1.9 mm long, subulate, a tuft of hairs at the base; grain 2.1-2.2 mm long, 1.2-1.3 mm wide, somewhat flattened; chromosome numbers unknown.

Observations

Phalaris amethystina and Phalaris caroliniana are morphologically very similar. The best differentiating character appears to be the presence of scabrous glume nerves in P. amethystina (Plate 8, f), a feature ordinarily lacking in P. caroliniana (Plate 9, f). In addition to this feature, the inflorescence of P. amethystina tends to be less dense than that of P. caroliniana; P. amethystina is a somewhat shorter plant than P. caroliniana. The wide separation in geographic ranges provides additional indication in favor of recognizing these as two separate species.

Cytology and cytogenetics

No living material of P. amethystina was available to the author for cytological studies. Chromosome numbers have not been reported for this species.

Nomenclature

A portion of the holotype of this species was examined in the United States National Museum.

The name Phalaris chilensis Presl. has occasionally been used for this species. Examination of the type specimen, which is in the National Museum, Praha, Czechoslovakia, showed it to be Phalaris angusta Nees ex Trin.

Distribution

The geographic origin of the specimens of the species studied by the author is indicated by the unshaded circles on the map in Figure 14.

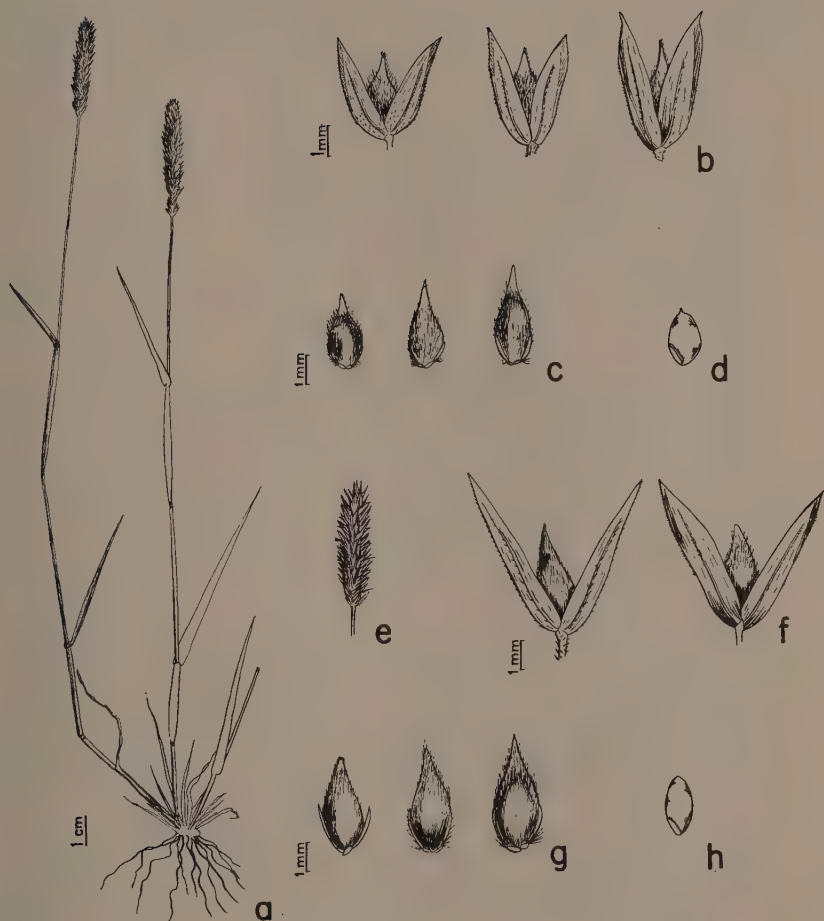


Plate 8. Phalaris platensis and Phalaris amethystina.

a-d. Phalaris platensis; a. habit, b. spikelets,
c. florets, d. caryopsis,

e-h. Phalaris amethystina; a. inflorescence, f. spikelets,
g. florets, h. caryopsis.

Specimens examined

CHILE: Aconcagua Prov., R.A. Philippi, 1888 (US); Coquimbo Prov., Claude-Joseph 4623 (US); O'Higgins Prov., Rancagua, Bertero 534 (holotype; clastotype is in US); Santiago Prov.: Santiago, Claude-Joseph Al21 (US); Santiago, Claude-Joseph 2346 (US); Valparaíso Prov.: Valparaíso, Claude-Joseph 3516 (US); E. Gunther 13 (US); Cumíng 458 (US); Autuco, Poppig 23 (MO); El Pangal, Limache, A. Garraventa 2837 (US).

13. Phalaris platensis

Phalaris platensis Henrard ex Heukels. Geïllustr. Schoolf. Nederl. 843. (1934) (Type in L)

Phalaris intermedia f. platensis Arechav. Las Gramineas Uruguayas 238 (1894)

Phalaris platensis (Arech.) Parodi in Valencia. Revista Argent. Agron. 4:298. (1937)

Phalaris arechavaletae Herter. Revista Sudam. Bot. 9:105. (1953)

Description

Annual; culms to 40 cm tall; panicle cylindrical, 3-8 cm long, longer panicles somewhat lobed at the base; glumes 3.9-5.1 mm long, more or less equal, acute, very narrowly winged near the apex or wingless, the keel and two lateral nerves scabrous; fertile floret 2.7-3.6 mm long, turgid, covered with spreading or appressed hairs except for the usually naked, sharply acuminate apex; sterile florets 2, 0.8-1.3 mm long, subulate, with a tuft of hairs at the base; grain 1.7-1.9 mm long, 1.0-1.2 mm wide, pale brown; chromosome number $2n=14$, the chromosomes ca. 3.4-5.6 μ long (Ambathsa, 1956).

Observations

This species is very closely allied morphologically with P. lemmonii from which it differs by its smaller spikelets and inflorescences. These differences are presented in Table 15.

As can be seen from this table, P. platensis averages somewhat smaller than P. lemmonii for the characters given. There are overlaps in extreme size values but the means are quite well set apart. In addition to these characters, the geographic ranges are quite distinct. P. platensis is limited to Argentina, Brazil, and Uruguay (rarely as an adventive in Netherlands); P. lemmonii occupies west coast valleys in North America. Henrard (1938) has noted Phalaris as one of many genera that possess species occurring in the southern United States and southern South America. The P. lemmonii-P. platensis complex, though P. lemmonii has a range in western rather than southern United States, seems to bear out this relationship. The spikelets and inflorescences of the two species are very similar, yet the rather stable quantitative differences, combined with the very distinct geographic distribution, leads one to believe that these constitute populations at the specific rather than infraspecific levels.

Cytology and cytogenetics

Ambathsa (1956) reported a chromosome number of $2n=14$ for this species. No material for cytological study was available to the author.

Table 15. Quantitative differences between Phalaris lemmonii Vasey and Phalaris platensis Henr.

Character		<u>lemmonii</u>	<u>platensis</u>
glume length	extreme	4.9 mm	3.9 mm
	mean	5.6	4.5
	extreme	6.7	5.1
fertile floret length	extreme	3.5 mm	2.7 mm
	mean	4.2	3.2
	extreme	5.1	3.6
sterile floret length	extreme	1.0 mm	0.8 mm
	mean	1.3	1.1
	extreme	1.6	1.3
inflorescence	extreme	4.0 cm	3.0 cm
	mean	7.6	4.8
	extreme	12.0	8.0
caryopsis length	extreme	2.1 mm	1.7 mm
	mean	2.2	1.8
	extreme	2.3	1.9

Nomenclature

The first legitimate specific name for this plant is that of Henrard as used by Heukels (1934). Even though it was published in a key, it satisfied the requirements of valid and effective publication.

In 1938, Henrard published a complete description and a discussion of P. platensis. The holotype, as cited in this later publication is in the Rijksherbarium, Leiden, Netherlands. The drawings of habit and spikelets (Plate 8, a, b) were made from the holotype.

Distribution

P. platensis is limited to the Parana and Uruguay River valleys in South America. The shaded circles in the map (Figure 14) show the geographic origin of the specimens examined by the author.

Little precise data are available concerning the habitat of the species. The label of the holotype (in L) reads "dans les prairies naturelles."

Specimens examined

ARGENTINA: Buenos Aires Prov.; Manantiales, L.R. Parodi 6625 (US); San Vicente, A. Burkart 13439 (US); Station de San Vicente, pres de Buenos Aires, B. Balansa, Dec. 5, 1875 (Holotype, in L. Herb. Lugd. Bat. 909.74...456); Villa Ortugar, L.R. Parodi 8968 (paratype in L, duplicate of paratype in US).

BRAZIL: Rio Grande do Sul Prov., Jard. Bot. Rio de Janeiro (US).

URUGUAY: Flores Dept., Sta. Adelaida, Gallinal 1122 (US); Florida Dept.: Estancia Rinconde, Santa Elena, Gallinal 5781 (US); Timota, Sta. Clara, Gallinal 2696 (US); Montevideo Dept., C. Arachavaleta (US); Soriano Dept., Gallinal, P.E. 802 (US).



Figure 14. Geographic distribution of Phalaris amethystina and Phalaris platensis.

14. Phalaris lemmonii

Phalaris lemmonii Vasey, Contrib. U.S. Nat. Herb. 3:42. (1892)
(Holotype in US)

Description

Annual; culms to 135 cm tall; panicle cylindrical, 4-12 cm long, 0.7-1.5 cm wide, usually lobed near the base, the 3 or 4 lobes up to 2 cm long; glumes subequal, 4.9-6.7 mm long, 0.9-1.1 mm wide, acuminate, sharp-pointed, not winged or only very slightly so, the 3 nerves scabrous; fertile floret 4.0-5.1 mm long, 1.2-1.6 mm wide, lanceolate, spreading pubescent (occasionally with the hairs appressed, especially in immature specimens) except for the acuminate tip; sterile florets 2, 1.0-1.6 mm long, narrow, appressed pubescent; grain 2.1-2.3 mm long, 1.1-1.3 mm wide, ovoid; chromosome number $2n=14$, the chromosomes ca. 3-5 μ long at diakinesis.

Observations

The most distinctive character of this species is the very plump, somewhat inflated fertile floret (Plate 9, c). Usually the floret is covered with spreading hairs although immature specimens occasionally have appressed pubescence. P. lemmonii seems most closely related to P. platensis. The differences between these two species have been discussed under P. platensis.

Cytology and cytogenetics

A chromosome number of $2n=14$ has been reported for Phalaris lemmonii Vasey by Parthasarathy (1939). The chromosome account obtained by the present author is presented in Table 16.

Table 16. Chromosome number obtained from pollen mother cells for Phalaris lemmonii Vasey.

Collection	Location	Chromosome number
Beecher Crampton 4826 Anderson voucher no. 1093	Calif., Yolo Co. Dunnigan	$2n=14$

Meiosis in the author's material appeared quite normal. Parthasarathy considers this species to be intermediate cytologically between the 12 and 14 chromosome types. Further consideration of this and other proposals are presented in the discussions of cytology of the genus.

Nomenclature

The holotype of this species is in the United States National Museum, Smithsonian Institution, Washington, D.C., and was examined by the author. This type represents the species as understood today. There are no other published names for this species.

Distribution

P. lemmonii is restricted to California in the western United States. Hitchcock (1950) gives the habitat as moist areas in the coastal valleys. Two collections from Victoria, Australia, apparently adventive, are in US. A map (Figure 15) shows the geographic origin of the specimens studied.



Figure 15. Geographic distribution of Phalaris lemmonii.



Plate 9. Phalaris lemmonii and Phalaris caroliniana.

a-d. Phalaris lemmonii; a. inflorescences b. spikelet
c. florets d. caryopsis

e-h. Phalaris caroliniana; e. inflorescence f. spikelet
g. floret h. caryopsis

Selected specimens examined

AUSTRALIA: Victoria: Baddaginnie, R.A. Black 1183.002 (US);
 Everton, R.A. Black 151 (US).

UNITED STATES: Arizona, J.G. Lemmon 403 (US 1011289); California: Alameda Co., Newark, J.B. Davy 1093 (US); Butte Co.: near Oroville in *Quercus lobata* belt, A.A. Heller 14360 (US); near Nelson, A.S. Hitchcock 5447 (US); Colusa Co., 4 miles east of Williams, R.S. Ferris 547 (MO); Kern Co., near Buena Vista Lake, A.A. Beetle 3992 (GH, MO); Los Angeles Co.: Inglewood, L. Abrams 3234 (GH, MO); Los Angeles, F.W. Gould 2281 (MO, US); Catalin Isl., Avalon, B. Trask, May, 1897 (MO); Madera Co., 4 miles east of Madera, R.F. Hoover 5282 (US); Marin Co., Black Point, J.T. Howell 21657 (F, ISC, US); Mendocino Co., Ukiah, P.B. Dickey D-881 (NDA); Merced Co., 7 miles north of Merced, R.F. Hoover 2099 (US); Placer Co., B. Crampton (ISC); Sacramento Co., B. Crampton 3352 (ISC); San Benito Co., R.W. Pohl 7263 (ISC); San Diego Co. T.S. Brandegee 3425 (F, GH, MO, US); San Joaquin Co., Kettleman-Terminus road, E.E. Stanford 1466 (MO); San Luis Obispo Co., 1 mile from Creston, R.F. Hoover 6788 (US); Santa Clara Co., Saratoga, R.L. Pendleton 1336 (US); Solano Co.: near Elmira, A.A. Heller 14551 (MO); near Vacaville, A.A. Beetle 1982 (GH); Sonoma Co., Santa Rosa, R. Hoffmann 737 (US); Stanislaus Co.: Adela, E.E. Stanford 857 (GH); 10 miles west of Modesto, R.F. Hoover 392 (US); 4 miles south of Oakdale, R.F. Hoover 77 (US); Woodward Reservoir, north of Oakdale, R.F. Hoover 1938 (US); Sutter Co., A.A. Beetle 3862 (GH, MO).

15. *Phalaris caroliniana*

Phalaris caroliniana Walt. Fl. Carol. 74. (1788) (lectotype in US)

Phalaris microstachys DC. Cat. Hort. Monsp. 131. (1813)

Phalaris americana Ell. Sketch Bot. So. Car. Ga. 1:101. (1816)

Phalaris occidentalis Nutt. Trans. Am. Philos. Soc. n.s. 5:144.

(1837) (Holotype in PH)

Phalaris trivialis Trin. Mem. Acad. St.-Petersb. Ser. 6. Pt. 2.

5:55. (1840)

Phalaris intermedia var. *microstachys* (DC.) Vasey Contr. U.S. Nat. Herb. 3:42. (1892)

Description

Annual; culms to 100 cm tall; panicle 1.0-7.0 cm long, 0.8-2.0 cm wide, ovoid to subovoid; spikelets somewhat spreading, the glumes not tightly imbricate; glumes 4.2-5.6 mm long, 0.8-1.5 mm wide, apex usually acute or acuminate, narrowly winged toward summit, the margin of the wing very finely scabrous, lateral nerves almost always glabrous, very rarely slightly scabrous; fertile floret 3.0-4.7 mm long, 0.9-1.8 mm wide, lanceolate, densely pubescent; sterile florets 2, 1.5-2.5 mm long, subulate, pubescent; caryopsis 2.0-2.3 mm long, 0.9-1.2 mm wide; somatic chromosome number $2n=14$, the chromosomes 3.0-4.4 μ long (Ambathsa, 1956).

Observations

The distinctions between P. caroliniana and P. angusta have been elaborated in the discussion of the latter species.

P. caroliniana and P. amethystina are morphologically quite similar. Some of the differences between these two species are presented in Table 13. The best means of separating the two is the presence or absence of scabrous pubescence on the glume lateral nerves. P. caroliniana almost always has glabrous glume lateral nerves; P. amethystina has rather heavily scabrous glume lateral nerves. In addition to these, there are some other less well-defined differences. The glumes of P. caroliniana are narrowly winged near the apex; glumes of P. amethystina are also winged, but the wing is extremely narrow and visible only after close scrutiny under 10X magnification. Glumes of P. caroliniana are rather broadly lanceolate (Figure 9, f); glumes of P. amethystina are narrowly lanceolate (Figure 8, f). The inflorescence of P. caroliniana is somewhat more compact, with the spikelets more densely imbricated than those of the inflorescence of P. amethystina. The geographic ranges of the two species are very distinct; P. caroliniana is found only in the southern one-third of the United States and the northern two-thirds of Mexico while P. amethystina is limited to a small area on the west coast of Chile. The morphologic differences, as well as the disjunct ranges seem to emphasize that these are two distinct species rather than varieties of a single species.

Vasey (1892) reduced De Candolle's P. microstachya (1813) to varietal status under P. caroliniana. Vasey's main differentiating features were the height of flowering culms and size of the inflorescence. Measurements were made on a large number of specimens to determine whether distinct populations could be delimited on the basis of these or other characters. Results showed that there were complete gradations in values for the characters that Vasey used in varietal distinction. None of the characters measured, which included glume length and width, fertile floret length and width, sterile floret length, inflorescence length and width, inflorescence length and width, and total height could be correlated with one another or with geographic origin of the collection to show any subspecific populations.

Cytology and cytogenetics

Brown (1950) and Ambathsa (1956) report a chromosome number of $2n=14$ for P. caroliniana. The author was unable to obtain any material suitable for cytological study.

Nomenclature

Hitchcock (1905) studied many of the grasses of the Walter herbarium which is in the Natural History section of the British Museum, South Kensington, London, England, and was unable to find any species of Phalaris represented in Walter's collections. He also noted that many of the types were missing from this collection. The author was able to examine photographs of the Walter herbarium which are deposited in the Gray Herbarium Library of Harvard University. None of the few grasses pictured were in Phalaris. From these lines of evidence it must be concluded that the holotype of this species is not available and probably lost.

Walter's description of Phalaris (1788, p. 74) is as follows:

33. Phalaris. Cal. 2-valvis, carinatus, longitudine aequalis, corallam includens.

caroliniana paniculata spicate ovata, petalis aristatis,
calycibus striatis

Walter's generic description leaves some doubt as to which genus he was referring. The characters provided by Walter are those of several different genera of grasses. When the specific description is also taken into account, the situation is somewhat clarified. Phalaris was the only genus available to Walter from the Carolinas that had an ovate, spikelike panicle, spikelets with equal, prominently-nerved carinate glumes which included the floret. The explanation of "petalis aristatis" is difficult. There seem to be three possible explanations of this phrase:

1. Walter was describing some species that was not even in Phalaris. Without the holotype this possibility can never be completely ignored; however, as pointed out in the above paragraph, there is no other species of the Carolina grass flora that would fit the description provided by Walter.

2. Walter was describing the two subulate sterile florets found in this taxon as either the "petals" themselves or as short awns of the "petals."

3. Walter was interpreting the acuminate fertile floret as being provided with a very short awn. Walter's use of the term "aristate" varies somewhat throughout Flora Caroliniana. In Vaccinium he uses it to describe the very short, mucronate appendages of the anthers, which, in V. stamineum, are 1 mm or less in length; in Alopecurus pratensis it is used to describe the awn, which may be 3 to 5 mm long. Some of the florets of P. caroliniana have quite prominent acuminate tips (see Figure 9, g) which Walter might conceivably have thought of as being aristate.

Even though the holotype is missing and the original description not conclusive, the circumstantial evidence seems to indicate that Phalaris caroliniana should be preserved as the name of this taxon. Muhlenberg (1817) used Walter's name, although, admittedly, it cannot be shown that Muhlenberg saw any of Walter's material.

In accordance with Article 7 of the International Code of Botanical Nomenclature, it becomes necessary to designate a neotype which will serve until such time as the holotype may be found. The following specimen is here designated as the neotype of Phalaris caroliniana Walter:

UNITED STATES: South Carolina, McCormick Co., in open field of moist bottomland about $1\frac{1}{3}$ miles due north of Clark Hill dam. Elevation about 200 feet. Wilbur H. Duncan 9468, May 4, 1949. United States National Museum specimen, accession no. 2075588. Deposited in US.

Phalaris intermedia Bosc ex Poiret has often been used as the name of this taxon. The original description (Poiret, 1810) calls for bulbous culm bases and a single sterile floret. Neither of these features are ever found in Phalaris caroliniana. If the original description is accurate, it would seem to refer to Phalaris aquatica. Until this name can be clarified by examination of the holotype it should be excluded from the synonymy of P. caroliniana.

Distribution

Phalaris caroliniana is found in the southern one-third of the United States and the northern two-thirds of Mexico. A map showing the geographic origin of the specimens studied is presented in Figure 16.



Figure 16. Geographic distribution of Phalaris caroliniana.

Hitchcock (1950) gives the habitat as old fields, sandy soil, and moist places. Collections made by the author were from gravelly hilltops in dry, well-drained soil.

Selected specimens examined

MEXICO: Sonora, Magdalena, J.N. Rose et al., 15078 (US); Sonora, ca. 31° x 109°, J.V. Santos 2027 (US).

UNITED STATES: Alabama, Montgomery, L.H. Pammel, May 26, 1921 (ISC); Arizona, Cochise Co., 6 mi. s.w. Apache, F.W. Gould and L.M. Pultz 3139 (US); Arkansas: Sebastian Co., Massard Prairie, D.M. Moore 480113 (US); Thos. Nuttall (Holotype of Phalaris occidentalis Nutt.) (PH); California: Butte Co., 8 miles north of Oroville, A.A. Heller 11307 (F, ISC, MO, US); Catalina Isl., Avalon, B. Trask, Mar., 1901 (MO, US); Georgia, Clarke Co., A. Cronquist 4364 (GH, MO, US); Kansas, Neosho Co., R.W. Pohl 7289 (ISC); Louisiana, Jefferson Par., Gretna, C.R.

Ball 327 (F.GH, MO, US); Mississippi, Jackson Co., Biloxi, A.S. Hitchcock 1074 (ISC, US); Missouri, Jasper Co., Webb City, E.J. Palmer 221 (MO); Nevada, Lincoln Co., Virgin R. valley, F.V. Coville and F. Funston 1924 (US); New Mexico, Grant Co., H.H. Rusby 457 (US); North Carolina, New Hanover Co., Wilmington, W.M. Canby, Octo., 1869 (US); Oklahoma, Kingfisher Co., Huntsville, L.A. Blankinship, May 20, 1896 (GH, MO, US); Oregon, Grant's Pass, T. Howell 221 (F, US); South Carolina: Georgetown Co., Georgetown Landing, C.A. Weatherby and L. Griscom 16413 (GH, US); McCormick Co., 1 1/3 miles north of Clark Hill Dam, W.H. Duncan 9468, May 4, 1949 (neotype of Phalaris caroliniana Walt.) (US); Tennessee, near West Tenn. Normal Teachers Coll., C.E. Moore 117 (US); Texas, Mitchell Co., R.W. Pohl 4479 (ISC); Virginia, Princess Anne Co., M.L. Fernald, L. Griscom, and Bayard Long 4547 (GH).

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APPENDIX

Contained in this appendix is a list of unidentified or excluded names. Unidentified names are followed by a question mark and, if necessary, a short explanatory phrase. Excluded names are followed by the name of the species to which they are referred. Evidence for the exclusion of the names is given by a brief statement or by reference to a page in the text of this paper on which that particular name is discussed. If a description is used as evidence, the author and date of publication are cited. Any pertinent information concerned with a particular name is also included.

Degraphis americana Ell. ex Loud. = ? nomen nudum. Loudon (1830).

Degraphis is apparently a misspelling of Digraphis as proposed by Trinius.

Digraphis arundinacea var. picta (L.) Pacher. Original description not seen. Hitchcock (1950) says this is presumably based on Phalaris arundinacea L. var. picta.

Phalaris alpina Jacq. = Phleum sp. Description, Jacquin (1786).

Phalaris altissima Desf. = ? nomen nudum. Listed as a synonym of Phalaris bulbosa by Desfontaines (1798).

Phalaris altissima Menezes non Desfontaines. = ? Description (Menezes, 1894) might refer to Phalaris aquatica L.

Phalaris ammophila (Host.) Link. = Ammophila arundinacea. Description of Ammophila arundinacea Host (1809).

Phalaris angusta Schlecht. = ? Description (Schlechtendahl, 1851) might refer to Phalaris minor Retz.

Phalaris arenaria Huds. = Phleum sp. Description, Hudson (1762).

Phalaris arenaria Pourr. = ? Original description not seen. Index Kewensis lists the location of the description as "Mem. Acad. Toul. 3:323. 1788." Grass nomenclature card file of the Smithsonian Institution says: "original published in 1783, not in U.S. Reprinted with annotations by Lagrange, Rel. Pourretional, Toulouse, 1855, paging of original not seen."

Phalaris aristata Schousboe ex Willd. = Phleum sp. Description, Willdenow (1801).

Phalaris aristata Gouan ex Beauv. non Schousboe ex Willd. = Polypogon monspeliensis. Published as synonym in index (Beauvois, 1812).

Phalaris ariculata Dicks. = ? nomen nudum, presumably a mistake for Phalaris utriculata L. Discussion, Dickson (1790).

Phalaris arundinacea f. coarctata Pahl ex Junge. = ? Original description not seen. Name in Junge (1913).

Phalaris aspera Lam. = ? Description, Lamarck (1783) seems to refer to Phleum.

Phalaris barrelieri Tenore. = ? Original description not seen. Index Kewensis says this = Koeleria villosa.

Phalaris bellardi Willd. = Phleum sp. Description, Willdenow (1801).

Phalaris bulbosa L. = Phleum sp. Examination of photograph (in GH) of type specimen.

Phalaris bulbosa var. aquatica (Willkomm) Perez-Lara (non L.) = ?

Description, which is based on P. aquatica as applied by Willkomm, might refer to Phalaris coerulescens.

- Phalaris bulbosa var. hirtiglumis Trabut. = ? nomen nudum. Trabut (1885).
- Phalaris caespitosa Du Petit-Thouars. = ? Description, Du Petit-Thouars (1811).
- Phalaris canadensis Raspail. = ? nomen nudum. Raspail (1825).
- Phalaris ciliaris Spreng. ex Jacks. nomen nudum. Jackson (1895).
- Phalaris ciliata Lag. = Phleum sp. Description, Lagasca (1816).
- Phalaris commutata Roern and Schult. (1817) See discussion under Phalaris aquatica in text.
- Phalaris cristata Forsk. = Polypogon sp. ? Description, Forskal (1775).
- Phalaris crypsoides D'Urv. = Maillea crypsoides ? Description, D'Urville (1822).
- Phalaris cuspidata Beauv. = ? pro syn. Listed as synonym of Chloa chloa cuspidata in index (Beauvois, 1812).
- Phalaris cuspidata Hort ex Steud. (non Beauv.) = ? nomen nudum. Listed as synonym of Phleum cuspidatum in Steudel (1841).
- Phalaris cylindrica Lam. and DC. = Phleum sp. Description, Lamarck and De Candolle (1805).
- Phalaris davesii Blake. = P. aquatica x P. minor. Not found in nature. See Blake (1956).
- Phalaris dentata L. fil. = Prionanthium dentatum ? Description, Linnaeus fil. (1781).
- Phalaris disticha Forsk. = Sporobolus sp. ? Description, Forskal (1775).
- Phalaris erucaeformis L. = Beckmannia erucaeformis. Examination of photograph (in GH) of type specimen.
- Phalaris erucoides L. ex Beauv. pro syn. Listed as a synonym of Beckmannia erucaeformis L. (Beauvois, 1812). Probably an error for erucaeformis.
- Phalaris explicata Link. = Heleochloa alopecuroides ? Description, Link (1799).
- Phalaris geniculata Sibth. = Heleochloa geniculata. Description, Sibthorp (1806).
- Phalaris glomerata Gueldenst. = ? Original description not seen. Index Kewensis lists the location of the description as "Reisen 2. 214."
- Phalaris hispida Thunb. = Arthraxon hispidus. Description, Thunberg (1784).
- Phalaris humulis Desv. = Phleum sp. Description, Desveaux (1831).
- Phalaris intermedia Bosc. ex Poiret. = Phalaris aquatica ? See discussion in text under P. caroliniana.
- Phalaris maritima Nutt. = Ammophila arundinacea. Description, Nuttall (1819).
- Phalaris mauritii Sennen in Sennen and Mauricio. nomen nudum. Sennen and Mauricio (1933).
- Phalaris mollis Du Petit-Thouars. = Polypogon intermedius ? Description, Du Petit-Thouars (1811).
- Phalaris monspeliensis Daveau = ? Daveau (1926) claims this to be a hybrid between P. arundinacea and P. nodosa (misapplied by Daveau to P. aquatica).
- Phalaris mucronata Desf. nomen nudum. Desfontaines (1815).
- Phalaris muricata Forsk. = Tragus racemosus. Description, Forskal (1775).

- Phalaris oryzoides L. = Leersia oryzoides L. Photograph (in GH) of type specimen.
- Phalaris paniculata (Huds.) Ait. = Phleum paniculatum. Based on Phleum paniculatum Huds.
- Phalaris pectinata Roth. = Phleum sp. ? Description, Roth (1821).
- Phalaris phleoides L. = Phleum sp. Photograph (in GH) of type specimen.
- Phalaris phleoides var. pratensis Lapey. = Phleum sp. Description, Lapeyrouse (1813).
- Phalaris picta Hort. ex Steud. nomen nudum. Steudel (1841).
- Phalaris pubescens Lam. = Koeleria villosa ? Description, Lamarck (1783).
- Phalaris sativa Pers. = Phleum sp. Description, Persoon (1805).
- Phalaris semineutra Roem. and Schult. = Poa semineutra. Description, Roemer and Schultes (1817).
- Phalaris semiverticillata Forsk. = Agrostis semiverticillata. Description, Forskal (1775).
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- Phalaris tenuifolia Hort. ex Steud. = ? nomen nudum. Steudel (1841).
- Phalaris tenuis Host. = Phleum sp. Description and illustration, Host (1802).
- Phalaris trigyna Host. = Phleum sp. Description and illustration, Host (1809).
- Phalaris utriculata L. = Alopecurus rendlei. See Eig (1937).
- Phalaris vaginiflora Forsk. = Heleochloa schoenoides. Description, Forskal (1775).
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- Phalaris villosa Michx. = Anthraenantia villosa. Description, Michaux (1803); see also Hitchcock (1908).
- Phalaris zizanioides L. = Vetiveria zizanioides. Photograph (in GH) of type specimen.

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¹ A circulating copy of each complete thesis is available in the Iowa State University Library, Ames, Iowa. Abstracts of these theses are published in Dissertation Abstracts. A microfilm or a photostat copy of a thesis may be purchased from Dissertation Microfilms, 313 N. 1st Ave., Ann Arbor, Michigan.

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